FURTHER NOTES ON PALAEONISCOID FISHES WITH A CLASSIFICATION OF THE CHONDROSTEI

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SYNOPSIS

A redescription is given of the type species of the genera *Gonatodus* Traquair, *Drydenius* Traquair, *Sphaerolepis* Frič, *Sceletophorus* Frič and *Phanerorhynchus* Gill. *Pseudogonatodus gen. nov.* is proposed for two species previously placed in *Gonatodus*. Eight new palaeoniscoid families are erected, the Gonatodidae, Osorioichthyidae, Gyrolepidotidae, Atherstoniidae, Lawniidae, Cosmolepididae, Brachydegmidae and Boreosomidae. One other new chondrostean family is proposed, the Habroichthyidae which belongs to the order Peltopleuriformes. The evolution of the Chondrostei is discussed and a classification of the Subclass given.

I. INTRODUCTION

Traquair (1877–1914), in his monograph on "The Ganoid fishes of the British Carboniferous formations", described the majority of the palaeoniscoids occurring in our Carboniferous strata. Subsequently Moy-Thomas and Dyne (1938) re-described and supplemented that portion of the fauna which occurred in the Lower Carboniferous rocks of Glencartholm. In an earlier paper (Gardiner 1963) I began the task of revising all the genera described by Traquair (1877–1914) except those adequately dealt with by Moy-Thomas & Dyne (1938) and this paper is intended to be a continuation of that work. In addition to genera described by Traquair I have redefined the Upper Carboniferous genus *Phanerorhynchus* Gill and redescribed two genera from the Upper Carboniferous of Czechoslovakia, *Sphaerolepis* Frič and *Sceletophorus* Frič.

Having examined almost all the palaeoniscoids, I have attempted a classification of the Palaeonisciformes, and, treated the much bigger problem of the evolution of the Chondrostei and its classification.

Later I hope to redescribe *Cryphiolepis* Traquair, *Acrolepis* Agassiz, *Myriolepis* Egerton and *Styracopterus* Traquair and then, in order to complete the survey, all the many species which were dealt with by Traquair will be re-examined in the light of my emended generic diagnoses.

II. SYSTEMATIC DESCRIPTIONS

Order **PALAEONISCIFORMES**

Family **GONATODIDAE** nov.

Diagnosis. Trunk deeply fusiform ; dorsal fin situated behind the middle of the back, more posterior in position than in *Elonichthys* Giebel. The remaining diagnosis as for the genus *Gonatodus*.

Remarks. From my description of *Gonatodus* it is clear that this genus does not belong in the Family Elonichthyidae where both Romer (1945 : 579) and Obruchev (1964 : 352) placed it ; further it does not fit into any other previously described family. A new family, Gonatodidae, is therefore erected to include this genus and the related genera *Drydenius* Traquair and *Pseudogonatodus* nov. The Gonatodidae later gave rise to both the Commentryidae Gardiner (1963 : 290) and the Amblypteridae Romer (Gardiner 1963 : 290).

Genus ***GONATODUS*** Traquair, 1877

1835 *Amblypterus* Agassiz (*partim*) **2**, 1 : 109.

Diagnosis (emended). Trunk deeply fusiform ; dorsal fin situated behind middle of back, partly in advance of, partly opposing, anal, both being large, triangular and approximately the same size. Dorsal contour arched in advance of dorsal fin. Paired fins large, pelvic pair midway between pectorals and anal. All fins with minute fulcra anteriorly and with rays closely articulated, so as to impart scale-like appearance to individual joints ; all rays distally bifurcated. Skull with suspensorium somewhat inclined, not so near vertical as in *Amblypterus*, moderately overhanging rostrum and relatively stout sclerotic ring. Opercular more than twice as deep as subopercular; suborbital series and dermohyal present. Branchiostegal rays numerous, skull roofing bones coarsely striated. Teeth closely set, of moderate size and in one series. Scales large with distinct peg and socket articulation, and ornamented with fine, oblique striae.

TYPE SPECIES. *Amblypterus punctatus* Agassiz.

REMARKS. Agassiz (1835, **2**, 1 : 109) in describing [the new species] *Amblypterus punctatus* used three specimens (R.S.M. 1878.18.4, R.S.M. 1878.18.6 and one in the Oxford University Museum) all of which are from the Calciferous Sandstone Series (Lower Carboniferous) of Wardie. Traquair (1877 : 265 ; 1877*b* : 555 ; 1877*c* : 60) realized that the species *Amblypterus punctatus* Agassiz was founded not only on two distinct species but that each of the two species belonged to different genera. For one of Agassiz's original syntypes (R.S.M. 1878.18.4) Traquair (1877) retained the specific name "*punctatus*" and used it to form the type of the new genus *Gonatodus*. To the other two syntypes of Agassiz (1835, **2**, 1, pl. 4*c*, figs. 3, 5) Traquair gave the new specific name *Elonichthys intermedius*. Traquair (1901 : 67) decided that *Elonichthys intermedius* was merely a variation of *Elonichthys robisoni* (Hibbert), and called it *Elonichthys robisoni* Hibbert var. *intermedius* Traquair. From an examination of the type material it is clear that Traquair was justified in separating the syntypes of Agassiz's *Amblypterus punctatus* into the two distinct species, *Gonatodus punctatus* (Agassiz) and *Elonichthys robisoni* (Hibbert).

The genus contains but the type species, the other two species referred to it by Traquair (1907), *Gonatodus parvidens* Traquair and *Gonatodus macrolepis* Traquair, are placed in a new genus, *Pseudogonatodus*.

Two other species that have in the past been included in this genus, *Gonatodus brainerdi* (Newberry 1873 : 346 ; 1890 : 125) and *Gonatodus ? toilliezi* (Koninck 1878 : 11), clearly belong elsewhere as already indicated by Traquair (1907 : 93). *Gonatodus brainerdi* from the Berea Grit of Ohio (Lower Carboniferous) is from its large size possibly a *Nematoptychius* ; while *Gonatodus ? toilliezi* from the Lower Carboniferous of Viesville, Belgium, has large fulcra and seems closer to *Canobius* than to *Gonatodus*.

Gonatodus punctatus (Agassiz)

(Text-figs. 1–4)

1835 *Amblypterus punctatus* Agassiz, **2**, 1 : 109, pl. 4*c*, fig. 4 (non figs. 3, 5–8).
1872 *Amblypterus anconoaechmodus* Walker : 119, pl. 1.
1877 *Gonatodus punctatus* (Agassiz) Traquair : 265.
1877*b* *Gonatodus punctatus* (Agassiz) ; Traquair : 555.
1877*c* *Gonatodus punctatus* (Agassiz) ; Traquair : 16, 60, pl. 2, figs. 4, 5.
1882 *Gonatodus punctatus* (Agassiz) ; Traquair : 546.
1890 *Gonatodus punctatus* (Agassiz) ; Traquair : 391.
1891 *Gonatodus punctatus* (Agassiz) ; Woodward : 434.
1903 *Gonatodus punctatus* (Agassiz) ; Traquair : 690, 700, 701.
1907 *Gonatodus punctatus* (Agassiz) ; Traquair : 93, pl. 19, text-figs. 2, 3*a*.
1907*b* *Gonatodus punctatus* (Agassiz) ; Traquair : 106, 114, 115, pl. 2, figs. 1, 2.
1925 *Gonatodus punctatus* (Agassiz) ; Watson : 859, text-fig. 27.
1954 *Gonatodus punctatus* (Agassiz) ; Waterston : 58.

DIAGNOSIS (emended). Fishes not exceeding 18·5 cm. in total length, body deeply fusiform, length of head contained slightly more than three and a half times and depth of body about two and three-quarter times in total body length (measured to bifurcation of caudal fin). Head short with bluntly rounded snout. Skull with two dermohyals, and teeth on jaws arranged in single closely set row. Scales of moderate size deeper than broad on flank and ornamented with distinct concentric ridges of enamel imparting delicate serration to posterior margin. Many ridges on dorso-posterior region of scales short and terminating in points before posterior margin is reached (Text-fig. 3).

HOLOTYPE. R.S.M. 1878.18.4, head and anterior half of fish wanting fins, from the Calciferous Sandstone Series (Lower Carboniferous) of Wardie, Edinburgh.

MATERIAL. In addition to the holotype, five complete fish, three tolerably complete fish, five skulls, isolated maxillae and scales in the British Museum (Natural History) and the Royal Scottish Museum, Edinburgh.

REMARKS. The specific name *punctatus* is rather an unfortunate one since the normal scale ornamentation consists of quite distinct, characteristic ridges of enamel. Only the occasional specimen has scales which show coarse punctures over the exter-

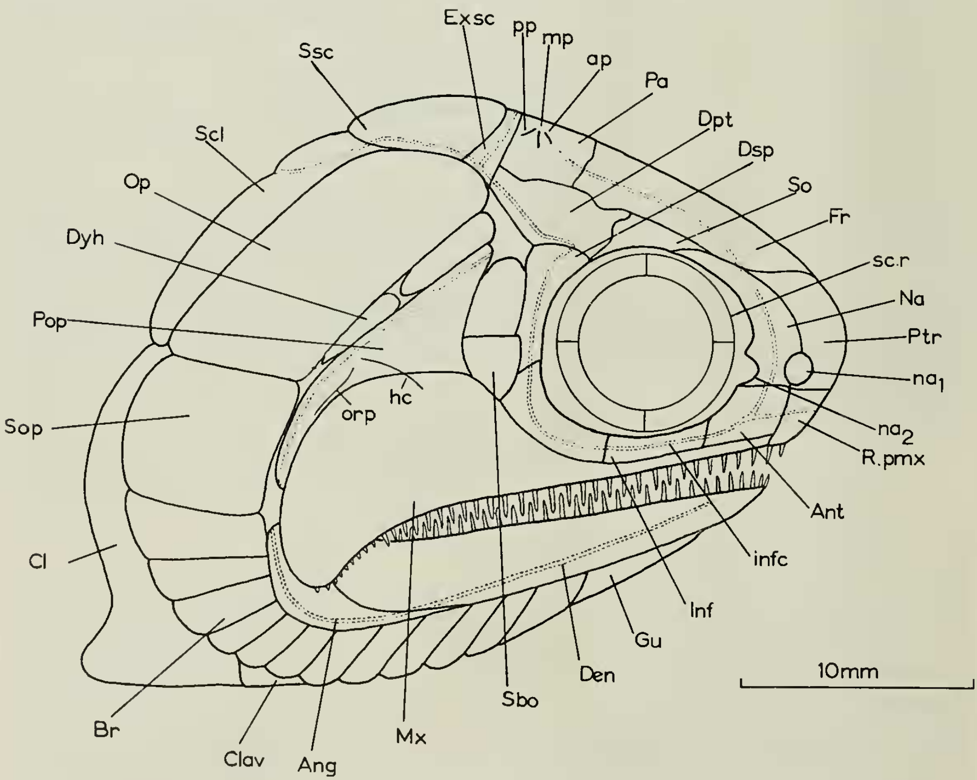

FIG. 1. *Gonatodus punctatus* (Agassiz). Reconstruction of skull in lateral view.

nal surface, and in these cases it is due to the resorption of most of the enamel layer, so that one is merely looking at the deeper layers of the scale, the punctures representing old blood vessel pathways.

I have already discussed the loss of ornamentation in the genus *Namaichthys* (Gardiner 1962 : 19) but without really emphasizing this process of resorption. Resorption has been noted in the Agnatha, the Dipnoi and the Crossopterygii, in skull roofing elements as well as scales, but has not so far been noticed in the Actinopterygii. Resorption of the scale ornamentation is most marked in the genus *Elonichthys* (*E. robisoni* (Hibbert), *E. semistriatus* Traquair) but I have also observed it in *Rhadinichthys*, *Drydenius* and *Gonatodus*. Normally the ornamentation of the scales in the posterior region is the first to undergo resorption, thus often the anterior part of the fish shows scales with a complex ornamentation of ridges and striae of enamel while the posterior scales are smooth apart from a distinct puncturing. In the past when the erection of species on scale ornamentation was a common practice this led to the naming of species which can often now be shown to be merely differences in resorption of an original scale type.

The scales from Wardie figured by Traquair (1901, pl. 9, figs. 6, 7) as *Elonichthys robisoni* (Hibbert) var. *intermedius* Traquair are identical with those of *Gonatodus punctatus* (Agassiz). Traquair believed that the sculpturing exhibited by these scales was due to the loss of the ganoine (enamel) layer. However, it is now clear that these figures of Traquair's (pl. 9, figs. 6, 7) represent the normal, ornamented, external scale surface of *Gonatodus punctatus*.

Description. *The skull.* The general shape of the skull can be seen from Text-fig. 1. Although the snout has a distinct rostrum, it is not nearly so pronounced as in the genera *Elonichthys* Giebel and *Nematoptychius* Traquair. The most characteristic features are the dermohyals and the arrangement and shape of the teeth.

The skull roofing bones are all ornamented with stout ridges of enamel, which in places give way to tubercles. On the parietals, frontals, dermopterotics and postrostral bones the ridges are broken up into elongated tubercles which run from the centre of ossification outwards. The ridges of enamel on the suprascapulars and extrascapulars are in the form of short striae which run concentrically. A similar ornamentation is seen on the suborbitals. The maxilla is covered by long ridges of enamel, partially broken up into segments, which sweep up and round the bone, running parallel with its posterior and superior borders. Ventrally the maxilla has more tubercles. On the subopercular the ridges are short and run more or less parallel horizontally, while on the opercular they are also short but run diagonally across the bone from the antero-dorsal corner.

The mandible is covered by long straight ridges of enamel which run along its entire length, a similar condition is seen on the branchiostegal rays, except that the ridges are much fewer in number.

The skull is relatively short and the suspensorium not too far off the vertical. The suprascapulars are broad and meet in the midline and the extrascapular series consists of the normal narrow, single pair of bones. The paired parietals are rectangular while the frontals are the longest bones in the skull roof and anteriorly meet both the postrostral and nasals. Laterally the frontal is bordered by the dermopterotic, supraorbital and nasal.

The lateral roof of the skull is comprised of two bones, the dermopterotic and the supraorbital. The dermopterotic is the larger and its dorsal margin is strongly emarginated at two points. Anteriorly the dermopterotic joins the shorter supraorbital, which separates it from the nasal. The nasal is short and broad and its lateral margin forms together with the dorsal margin of the antorbital a distinct notch, which indicates the position of the posterior nostril. The anterior nostril lies between the nasal and the postrostral. Posteriorly the nasal joins the frontal and supraorbital. The postrostral is another stout, broad bone, moderately convex anteriorly, which meets ventrally the paired, toothed, rostro-premaxillaries. Posterior to the rostro-premaxillary is a stout antorbital, which does not enter into the jaw margin.

There are two members of the infraorbital series while the dermosphenotic is long and forms a considerable portion of the upper posterior margin of the orbit. The suborbital series consists of two rounded bones, the upper of which is the larger.

The maxilla is of the normal palaeoniscoid pattern and curves slightly upwards before it meets the rostro-premaxillary. The ventral margin bears teeth along its entire length ; the teeth are nearly uniform, long and stout and arranged in a single closely set row. Each tooth has a distinct terminal cap. The preopercular is a high bone with its posterior margin much nearer to the vertical than that of *Elonichthys*. Behind the preopercular and filling the gap between it and the opercular lie two wedge-shaped dermohyals. However in one specimen, R.S.M. 1926.57.16, at least three dermohyal elements are present. The opercular is rectangular in outline and more than twice as high as the subopercular. Preceding the subopercular are twelve to thirteen broad branchiostegal rays and a large median gular. The orbit is supported by a stout sclerotic ring composed of four elements.

The lower jaw. Posteriorly the lower jaw is much deepened due to the upward extension of the dentary and to the presence of a surangular, much as in *Amblypterus*. The outer surface of the jaw is formed by a stout angular posteriorly while the remainder is made up of the large dentary. The dentary also forms part of the inner surface anteriorly. The remainder of the inner surface is covered by a large prearticular. The upper border of the dentary supports a single series of stout, tall, rather closely set teeth. There is a coronoid series which overlaps the dorsal, internal portion of the dentary. Posteriorly the articular portion of Meckel's cartilage is ossified.

The palate. The palate has already been figured by Watson (1925, text-fig. 27). The quadrate is stout and the ectopterygoid small in comparison with the much longer entopterygoid. The metapterygoid is well ossified as is the remainder of the suprapterygoid series which forms a single, large ossification. Anteriorly the suprapterygoid is notched for the passage of the maxillary and mandibular divisions of the fifth nerve. The palatine is a mere sliver of bone, but both it and the ectopterygoid bear a single row of large teeth. Anteriorly there is a pair of toothed vomers.

The neurocranium. Apart from the parasphenoid, little can be made out. The

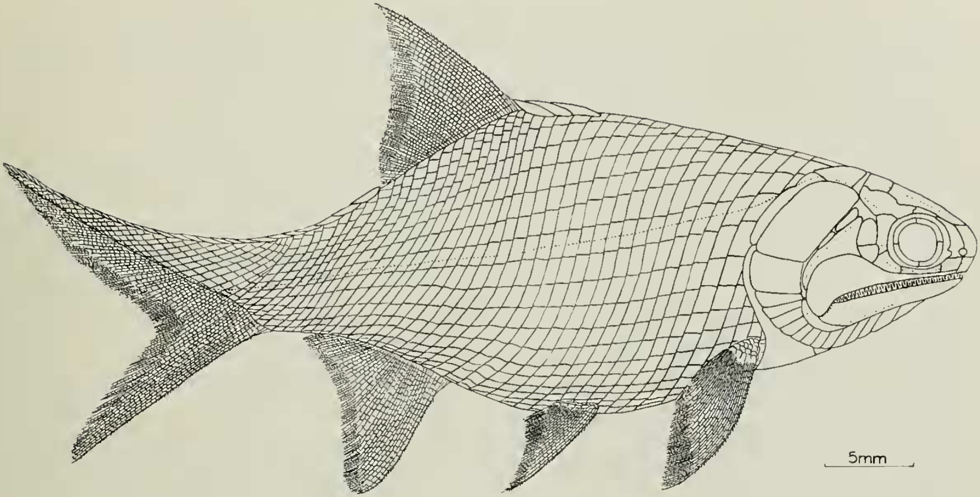

FIG. 2. *Gonatodus punctatus* (Agassiz). Restoration of whole fish.

parasphenoid is short and broad as in *Pteronisculus* White, with a well marked basipterygoid process (see Traquair 1877*c*, pl. 2, fig. 5).

The paired fins and their girdles. The pectoral girdle consists of a supracleithrum which stretches down to the junction between the opercular and subopercular, an elongate cleithrum and a stout clavicle.

The ornamentation on the supracleithrum is delicate, with ridges of enamel which branch to a limited degree and run across the bone rather than following its length as they do on the cleithrum.

The pectoral fin is large with between thirty and thirty-two lepidotrichia. The rays are smooth and the articulations tolerably close, especially in the finer rays of the posterior part of the fin. However, in the most anterior fin rays the articulations are quite far apart. The base of the fin is covered by a series of small scales.

The pelvic fin is somewhat smaller with between eighteen and twenty rays, all closely articulated.

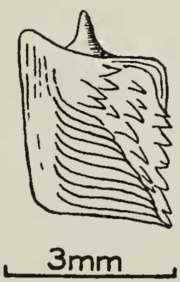

FIG. 3. *Gonatodus punctatus* (Agassiz). Anterior flank scale.

The unpaired fins. Both dorsal and anal fins are triangular and of similar size with between forty and forty-five rays. The articulations of the rays in both fins are so close that the joints of the base of the fins look most scale-like. The fin rays are smooth apart from a single longitudinal furrow.

The caudal fin is heterocercal, inequilobate and deeply cleft.

The squamation. The scales of the flank are slightly higher than broad and at the deepest point of the body number around twenty-two rows. They possess a distinct peg and socket articulation and in proportion to body size the scales are large. The ornamentation is most distinct consisting of prominent ridges of enamel (Text-fig. 3). The ridges follow the postero-ventral margin and also the dorsal margin. There is a triangular portion posteriorly where short, pointed, overlapping tubercles pass back towards the hind margin which is pectinated.

There are three large ridge scales in front of the dorsal fin, and the ridge scales of the axial lobe start immediately behind the dorsal fin.

Scale structure. The general structure of the scale can be seen from Text-fig. 4. Aldinger (1937 : 212) has already pointed out the similarity of the scale structure to that seen in *Elonichthys*. The canal plexus of the dentine layer is composed of horizontal and radial canals (vascular). The horizontal canals bear tree-like dentine tubules. The radial canals penetrate obliquely through the bony lamellae from the scale margins, sending feeder branches upwards to connect with the horizontal canals. Thus the radial canals are for the most part at a much deeper level than the horizontal canals. A few canals (canals of Williamson) penetrate upwards from the centre of the base of the scale to connect with both the radial canals and the horizontal

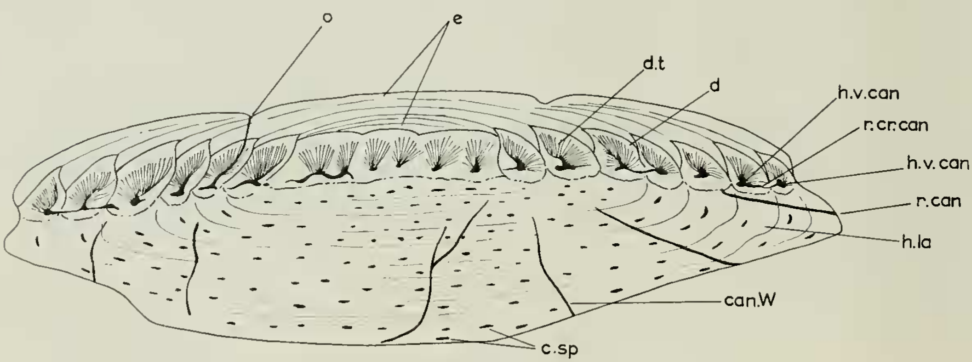

FIG. 4. *Gonatodus punctatus* (Agassiz). Dorso-ventral cross section through mid-lateral scale. ×45. From B.M.N.H. P.11704.

canals. The horizontal canals often connect with one another by means of radial cross connections. Occasionally ascending branches of the dentine canal plexus penetrate the external enamel layer (as in *Elonichthys*). Bone cells are present in the bony lamellae but no fibres of Sharpey were observed.

In overall structure the scale of *Gonatodus punctatus* is close to that of *Elonichthys*.

Locality and horizon. Apparently confined to the Calciferous Sandstone Series (Lower and Middle Visean) at the base of the Scottish Lower Carboniferous. It is recorded from ironstone nodules at Wardie, Edinburgh, from Gullane, East Lothian and from Pitchorthy, Fifeshire. One specimen, also in an ironstone nodule, is recorded from Collinton, Edinburgh (B.M.N.H. P.11704).

Genus ***PSEUDOGONATODUS*** nov.

1877 *Gonatodus* Traquair (*partim*) : 271.
1882 *Gonatodus* Traquair (*partim*) : 546.

Diagnosis. Body fusiform ; dorsal fin placed rather far back (nearer to tail than in *Gonatodus* Traquair), partly in advance of, partly opposing the anal but giving appearance of being almost opposite it. Both fins of moderate size, triangular, smaller than in *Gonatodus*. Paired fins large, with stout rays, pelvics placed nearer to anal than to pectorals ; caudal fin deeply cleft and inequilobate. All fins with prominent fulcra anteriorly and rays closely articulated and distally bifurcated. Skull with almost vertical suspensorium (as in *Amblypterus*) and rostrum not pronounced. Opercular less than one and three-quarter times as deep as subopercular. Suborbital and dermohyal series present. Branchiostegal rays numerous, skull roofing bones and cheek bones ornamented with coarse, stout ridges of enamel ; teeth of variable size but in single series. Scales rhomboid and large (larger than in *Gonatodus*), ornamented with fine striae and distinct punctations.

Type species. *Gonatodus parvidens* Traquair.

Remarks. Traquair (1877 ; 1882) placed three species in the genus *Gonatodus*, *G. punctatus* (Agassiz), *G. macrolepis* Traquair and *G. parvidens* Traquair. It is now clear that *G. parvidens* and *G. macrolepis* are not congeneric with *G. punctatus* and the new genus *Pseudogonatodus* is here proposed for them. For the type species I have selected *G. parvidens* since this is by far the better known of the two species.

Pseudogonatodus parvidens (Traquair)

(Text-figs. 5, 6)

1881 *Gonatodus* sp., Traquair : 315 (name only)
1882 *Gonatodus parvidens* Traquair : 546.
1890 *Gonatodus parvidens* Traquair ; Traquair : 392.
1891 *Gonatodus parvidens* Traquair ; Woodward : 435, pl. 16, fig. 7.
1903 *Gonatodus parvidens* Traquair ; Traquair : 695, 696, 700, 701.
1907 *Gonatodus parvidens* Traquair ; Traquair : 99, pl. 21, text-fig. 3*c*.
1937 *Gonatodus parvidens* Traquair ; Aldinger : 212, text-fig. 55.
1954 *Gonatodus parvidens* Traquair ; Waterston : 57.

Diagnosis (emended). Fishes not exceeding 22 cm. in total length, body fusiform, length of head contained little over five times and greatest depth of body four times in total body length. Suspensorium nearly vertical, head short and with bluntly rounded snout. Maxilla of distinctive shape, high posteriorly. Single large suborbital present. Teeth on jaws very small, arranged in single closely-set row.

Scales large in proportion to body size, deeper than broad on the flank, feebly ornamented with few striae and exhibiting coarse punctations. Posterior borders of scales delicately serrated.

LECTOTYPE, here chosen. R.S.M. 1926.57.19, a tolerably entire fish from the Borough Lee Ironstone, Edge Coal series, Loanhead, near Edinburgh.

MATERIAL. In addition to the lectotype, about twelve almost complete fish, eight bodies wanting skull, two skulls, isolated maxillae, scales and jaws in the British Museum (Natural History) and the Royal Scottish Museum, Edinburgh.

REMARKS. *Pseudogonatodus parvidens* (Traquair) was first recognized by Traquair (1882 : 546) as a distinct species using detached maxillary bones from the Borough Lee Ironstone supplemented by more or less entire fish from the same locality. The

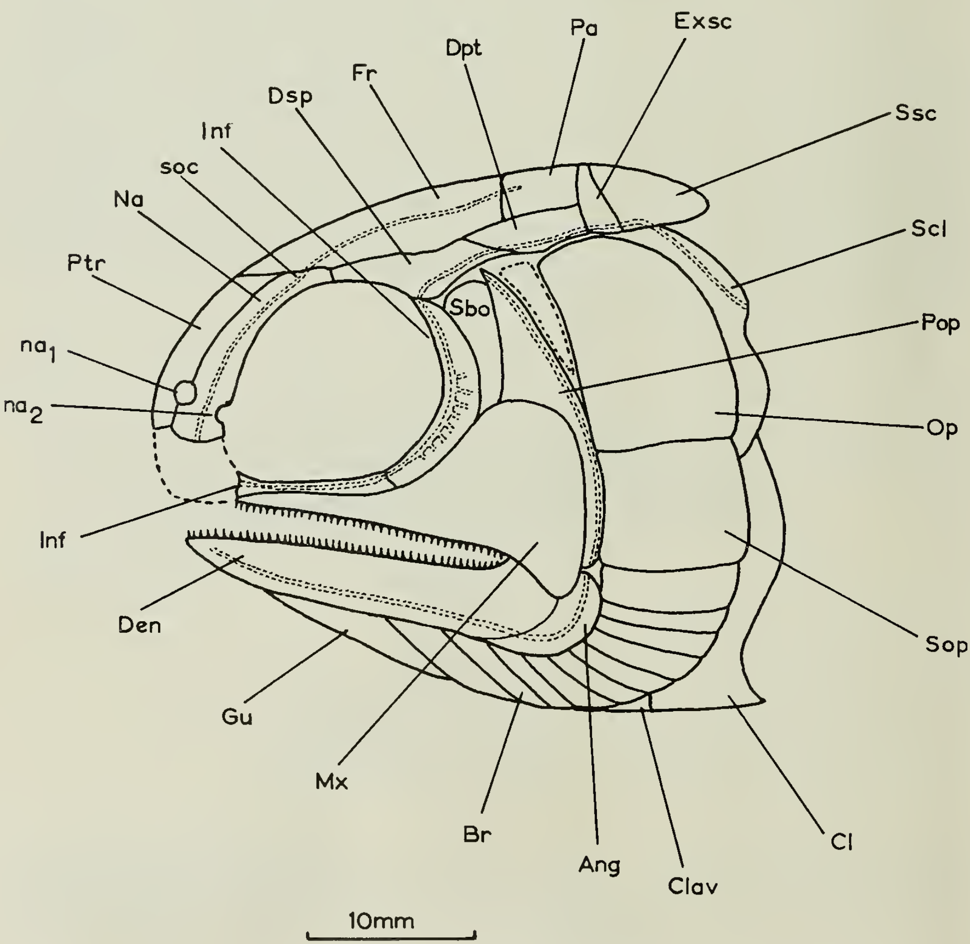

FIG. 5. *Pseudogonatodus parvidens* (Traquair). Reconstruction of skull in lateral view.

maxilla is perhaps still the most characteristic feature by which the species can be recognized.

The ornamentation of the scales, with few striae and many punctations, is misleading and is once more the result of resorption of superficial enamel. It would seem that if younger, better preserved specimens were available a more extensive ornamentation comprising ridges of enamel would be apparent.

Description. *The skull.* The bones of the skull and course of the sensory canals are shown in Text-fig. 5. The more distinctive features are the almost upright suspensorium and the shape of the maxilla.

The skull roofing bones are all ornamented with stout, long ridges of enamel, more pronounced than in *G. punctatus*. The ridges more or less follow the length of the bones with a few interspersed tubercles on the frontals and the anterior end of the postrostral. The ridges on the maxilla are likewise prominent, running up and round the bone parallel with the posterior and superior borders. Even on the anterior end of the maxilla short ridges run upwards from the ventral surface. On the sub-opercular the ridges run parallel from front to back while on the opercular they run diagonally across from the antero-dorsal corner. On the mandible the ridges of enamel are again stout and run along its entire length. Similarly on the gular plate and branchiostegal rays stout long striae run along the long axis of the bones.

The skull is short and the suspensorium almost upright (nearer the vertical than in *Gonatodus*). The suprascapulars are of normal size and are preceded by a narrow pair of extrascapulars. The parietals are square in outline and the frontals are very large. Anteriorly the frontal meets both postrostral and nasal. Laterally the parietals and frontals are bordered by the dermopterotic and dermosphenotic. The dermopterotic is roughly rectangular but anteriorly is produced into a point. The dermosphenotic is larger than the dermopterotic and anteriorly meets the nasal. Both the nasal and the postrostral are long, stout bones of somewhat the same proportions as in *Amblypterus*. The position of the anterior nostril is clearly marked between the postrostral and nasal while that of the posterior is indicated by a distinct notch in the nasal. Both nostrils are borne rather high up on the snout as in *Amblypterus*. The most anterior portion of the snout is not clearly preserved in any of the specimens I have examined.

There are two members of the infraorbital series, the second of which is much expanded. The infraorbital sensory canal on its passage through this second infraorbital gives off many short branches posteriorly. The suborbital series consists of one bone only which is much higher than broad.

The maxilla is of unusual shape, high posteriorly and with an almost vertical posterior border. The ventral margin bears very small teeth along its entire length, arranged in a single closely set series. Although small, the teeth are of the same shape and arrangement as in *G. punctatus*. The preopercular is a high bone with a gap between it and the opercular. Although it cannot be seen with certainty, a dermohyal element appears to fill this gap. The opercular is almost rectangular, less than one and three-quarter times as high as the subopercular. Below the subopercular are ten branchiostegal rays and a large median gular. A sclerotic ring probably supported the eye.

The lower jaw. Posteriorly the lower jaw is much expanded, giving a high prominence, much as in *Amblypterus* and *Gonatodus*. Anteriorly the jaw is much shallower. The angular bone does not extend very far along the ventral jaw surface and the articular region is ossified. The dentary bears a single series of small closely set teeth. Anteriorly the dentary forms part of the inner jaw surface while the remainder of the inner surface is covered by the prearticular and a coronoid series.

The palate. Although little could be made out, both the ectopterygoid and palatine bear numerous small teeth.

The unpaired fins and their girdles. The supracleithrum extends ventrally beyond the junction of the opercular with the subopercular, the cleithrum is elongate and the clavicle stout. The ornamentation of both supracleithrum and cleithrum is distinct and consists of elongate striae of enamel which follow the long axis of the bone.

The pectoral fin is large with seventeen to nineteen lepidotrichia.

The pelvic fin is smaller with only twelve to thirteen fin rays.

The unpaired fins. Both dorsal and anal fins are triangular with the dorsal fin placed well back. The number of rays cannot be determined with complete accuracy but is not many more than twenty in either fin. The fulcra are distinct, larger than in *Gonatodus*.

The caudal fin is heterocercal, inequilobate and deeply cleft.

All the fin rays are closely articulated and distally bifurcated.

The squamation. The scales are higher than broad on the flank and at the deepest part of the body number around ten to twelve rows. Thus in proportion to body size the scales are large (larger than in *Gonatodus*). The ornamentation can be seen from Text-fig. 6 and consists of two or three striae following the antero-ventral border and of serrations (fine denticulations) posteriorly. The main portion of the scale is smooth apart from numerous punctations.

Scale structure. The scale structure of *Pseudogonatodus parvidens* (Traquair) has already been partly dealt with by Aldinger (1937, fig. 55). In general it resembles that of *Elonichthys*. For a more complete description of the scale structure of *Pseudogonatodus* see under *Pseudogonatodus macrolepis* (Traquair).

LOCALITY AND HORIZON. Carboniferous of Scotland, Namurian to Ammanian (Westphalian A). From the Edge Coal series (Borough Lee Ironstone) at Borough Lee, Loanhead, Wallyford, Possil and Lochgelly. Also from the South Parrot coal seam, Niddrie.

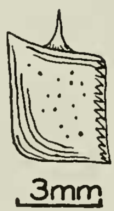

FIG. 6. *Pseudogonatodus parvidens* (Traquair). Anterior flank scale.

Pseudogonatodus macrolepis (Traquair)

(Text-figs. 7–9)

1877 *Gonatodus macrolepis* Traquair : 271.
1877*b* *Gonatodus macrolepis* Traquair : 556.
1881 *Gonatodus macrolepis* Traquair ; Traquair : 35 (name only).
1882 *Gonatodus macrolepis* Traquair ; Traquair : 546.
1890 *Gonatodus macrolepis* Traquair ; Traquair : 391.
1891 *Gonatodus macrolepis* Traquair ; Woodward : 435, pl. 16, fig. 8.
1903 *Gonatodus macrolepis* Traquair ; Traquair : 692, 694, 700, 701.
1907 *Gonatodus macrolepis* Traquair ; Traquair : 97, pl. 20, figs. 9–14, text-fig. 3*b*.
1937 *Gonatodus macrolepis* Traquair ; Aldinger : 212.
1954 *Gonatodus macrolepis* Traquair ; Waterston : 57.

DIAGNOSIS (emended). Fishes not exceeding 18 cm. in total length, body fusiform, length of head contained five times and greatest depth of body little more than four times in total body length. Maxilla of distinctive shape, postero-ventral margin being sharply bent downward, so much so that main blade of maxilla is much higher than broad (see Text-fig. 7). Teeth on jaws large, arranged in single row but of same shape and disposition as in *Pseudogonatodus parvidens* and *Gonatodus punctatus*.

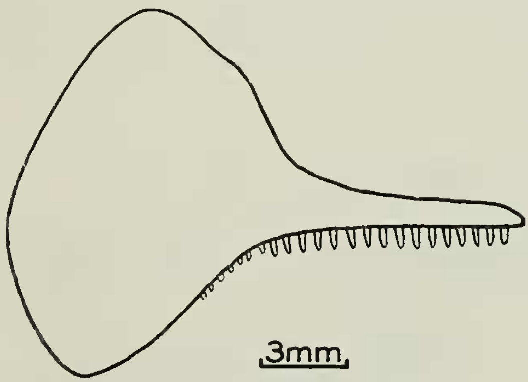

FIG. 7. Maxilla of *Pseudogonatodus macrolepis* (Traquair).

Scales large in proportion to body size, numbering around ten to twelve rows at deepest part of body. Scales deeper than broad on flank, rhomboidal, feebly ornamented with few traces of striae and with finely serrated posterior border. Remainder of scale surface smooth apart from delicate punctures (Text-fig. 8). Again resorption seems to have occurred. Large ridge scales preceding caudal fin.

LECTOTYPE. R.S.M. 1926.57.20 and counterpart B.M.N.H. P.11648, an imperfect fish from the Gilmerton Ironstone, Lower Carboniferous Limestone series, Venturefair Pit, Gilmerton, near Edinburgh. Designated as the " type specimen " by Traquair (1907, pl. 20, fig. 9).

MATERIAL. In addition to the lectotype, six tolerably complete fish, four bodies without heads, three isolated maxillae and one dentary in the British Museum (Natural History) and the Royal Scottish Museum, Edinburgh.

REMARKS. Apart from the shape of the maxilla and the large teeth, this species is very similar to the type species.

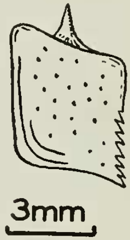

FIG. 8. *Pseudogonatodus macrolepis* (Traquair). Anterior flank scale.

Scale structure. The fine structure of the scale can be seen in Text-fig. 9. In most respects it is similar to that already described in *Gonatodus punctatus* (Agassiz). The arrangement of the canals in both the dentine and the bony lamellae is identical with those in *Gonatodus punctatus*. However, in the scale of *Pseudogonatodus macrolepis* there is a great concentration of fibres of Sharpey which was not observed

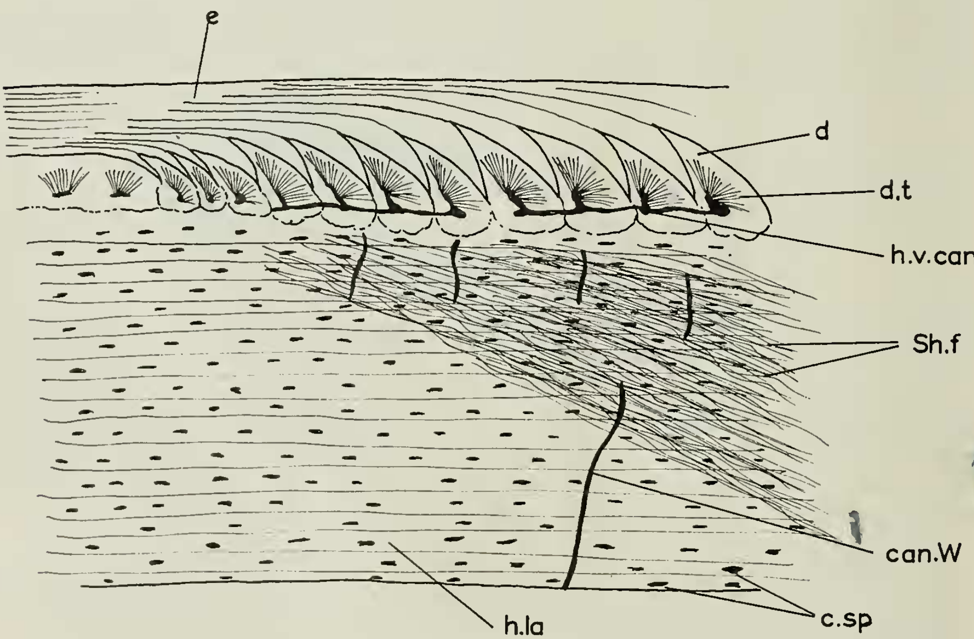

FIG. 9. *Pseudogonatodus macrolepis* (Traquair). Dorso-ventral cross section through mid-lateral scale. ×100. From B.M.N.H. P.11648.

in *Gonatodus punctatus*, while there appears to be a greater number of cell spaces in the bony lamellae of *Pseudogonatodus macrolepis*.

The structure of the scale of *Pseudogonatodus* is close to that of both *Gonatodus* and *Amblypterus*.

LOCALITY AND HORIZON. Lower Carboniferous (Middle to late Visean). A few specimens from the Calciferous Sandstone of Straiton, the remainder from the Gilmerton Ironstone, Venturefair Pit, Gilmerton.

Genus ***DRYDENIUS*** Traquair 1890

1877*c* *Microconodus* Traquair : 12, 33 (name only, but see also Traquair 1907 : 103).
1888 *Gonatodus* Traquair (*partim*) : 252.

DIAGNOSIS (emended). Body fusiform, dorsal fin placed opposite space between pelvics and anal, both dorsal and anal fins triangular, anal smaller. Caudal fin heterocercal, inequilobate. Pelvics and pectorals with less than ten rays. All fins have small number of rays articulated and distally bifurcated ; small fulcra fringe leading edges. Suspensorium appears to have been almost vertical. Teeth on both maxilla and dentary in single series, stout and closely set. Coronoid series also bearing large teeth set in more than one row. Scales very large in proportion to body size, deeper than broad on flank and ornamented with occasional striae.

TYPE SPECIES. *Drydenius insignis* Traquair.

REMARKS. This genus contains but two species. *D. insignis* Traquair and *D. molyneuxi* (Traquair), both of which were placed in it by Traquair (1890 : 392 ; 1907 : 102). The large scales, stout but few fin rays and the presence of coronoid teeth make the genus readily identifiable. An interesting feature of *Drydenius* is that the maxilla has begun to grow down around the peg-like teeth and partially encases them proximally. In the later genus *Paramblypterus* Sauvage which was derived from the Gonatodidae the maxilla completely encases the teeth apart from the distal tips.

Drydenius insignis Traquair

(Text-figs. 10, 11)

1890 *Drydenius insignis* Traquair : 392, 399.
1891 *Drydenius insignis* Traquair ; Woodward : 437.
1903 *Drydenius insignis* Traquair ; Traquair : 695, 700, 701.
1907 *Drydenius insignis* Traquair ; Traquair : 101, pl. 22, figs. 5–9.
1954 *Drydenius insignis* Traquair ; Waterston : 59.

DIAGNOSIS (emended). Fishes not exceeding 13 cm. in total length, body fusiform, dorsal fin opposite space between pelvics and anal. Caudal fin heterocercal and deeply cleft. Length of head contained little more than five times and greatest depth of body four and a half times in total body length. Scales denticulated posteriorly, surface smooth with no ornamentation apart from fine punctations (see Text-fig. 11).

LECTOTYPE. Selected by Waterston (1954 : 59). R.S.M. 1950.38.85, a splenial bone from the Borough Lee Ironstone, Edge Coal Series ; Loanhead near Edinburgh.

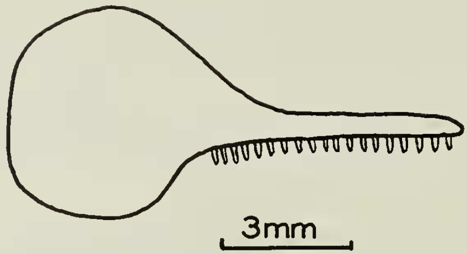

Fig. 10. Maxilla of *Drydenius insignis* Traquair.

Material. In addition to the Lectotype, two complete fish, one body wanting head, two isolated maxillae, and two splenials in the British Museum (Natural History) and the Royal Scottish Museum.

Description. The external skull bones, including the jaws, are all ornamented with long, relatively stout striae of enamel which more or less follow the length of the bones. The suspensorium appears to be almost upright.

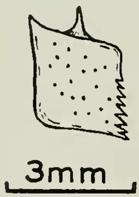

Fig. 11. *Drydenius insignis* Traquair. Anterior flank scale.

On the coronoid series is a single row of very large, stout teeth, and internal to this there are often numerous small granular teeth. The palatal bones also appear to be clothed with small granular teeth. The large teeth on the coronoid are larger than the teeth on the dentary or maxilla.

The maxilla is of unusual shape and quite diagnostic. The main blade is small in comparison with the normal palaeoniscoid maxilla, and not as high as in *Pseudogonatodus macrolepis*. The teeth on the maxilla are large and stout and in a single series along the anterior two-thirds of the bone (Text-fig. 10).

The pectoral fin (R.S.M. 1890.78.18) has from eight to ten lepidotrichia, and is short-based. The pelvic fin has some eight or nine stout rays while the dorsal fin is the largest with from twenty to twenty-two rays. The anal fin has fifteen rays.

The scales are large in proportion to body size, at the deepest part of the body numbering between nine and ten rows. Scales ornamented with striae and punctations; hinder margin denticulated.

Locality and horizon. Carboniferous of Scotland, early Namurian (E_1–E_2). From the Borough Lee Ironstone at Borough Lee and Loanhead. (The Borough Lee Ironstone is a member of the Edge Coal or Middle Carboniferous Limestone series.)

Drydenius molyneuxi (Traquair)

(Text-figs. 12–15)

1877c *Microconodus molyneuxi* Traquair : 33 (name only).
1888 *Gonatodus molyneuxi* (Traquair) Traquair : 252.
1890 *Gonatodus molyneuxi* (Traquair) ; Ward : 178, pl. 6, fig. 11.
1891 *Gonatodus molyneuxi* (Traquair) ; Woodward : 436, 437.
1905 *Gonatodus molyneuxi* (Traquair) ; Ward : p. 302, pl. 6, fig. 2.
1907 *Drydenius molyneuxi* (Traquair) Traquair : 102, pl. 20, figs. 6–8.
1919 *Drydenius molyneuxi* (Traquair) ; Pruvost : 425, 426, pl. 29, figs. 6–17.
1930 *Drydenius molyneuxi* (Traquair) ; Pruvost : 130, pl. 1, fig. 5.
1943 *Drydenius molyneuxi* (Traquair) ; Heide : 39, pl. 3, fig. 5*a–f*.
1954 *Drydenius molyneuxi* (Traquair) ; Waterston : 59.
1958 ?*Drydenius* sp. Vangerone : 472, pl. 23, fig. 3.

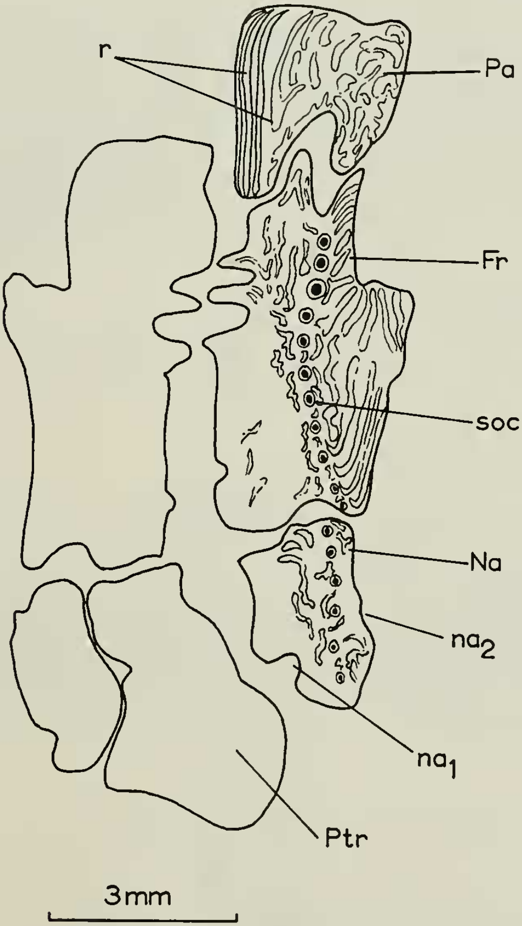

FIG. 12. *Drydenius molyneuxi* (Traquair). Dorsal view of skull roofing bones. From B.M.N.H. P.7973 & counterpart.

DIAGNOSIS (emended). Fishes not exceeding 7 cm. in total length, body fusiform. Length of head contained four a half times, and greatest depth of body a little over four times, in total body length. Blade of maxilla rounded dorsally. Scales very finely denticulated posteriorly (far more denticulations than in *D. insignis*), with fine striations running up diagonally from these denticulations. These fine striae only on posterior third of scale ; anterior portion with few punctures and an occasional stria following anteroventral margin (Text-fig. 14).

LECTOTYPE, here chosen. B.M.N.H. P.7973 and counterpart P.7976, a tolerably complete fish from the Deep Mine Ironstone (Westphalian C), Longton, Staffordshire.

MATERIAL. In addition to the lectotype, five comparatively complete fish, four bodies without skulls, and isolated lower jaws in the British Museum (Natural History) and the Royal Scottish Museum.

DESCRIPTION. The external skull bones including the jaws are ornamented with stout ridges of enamel, which are more or less contorted and not in straight lines as in *D. insignis*, *Pseudogonatodus* and *Gonatodus*. The orbit is large and the snout rounded. The suspensorium is upright and the lower jaw short and stout. The sutures between the frontals and between the frontals and parietals are digitate (Text-fig. 12). The maxilla is of characteristic shape (Text-fig. 13) with a larger

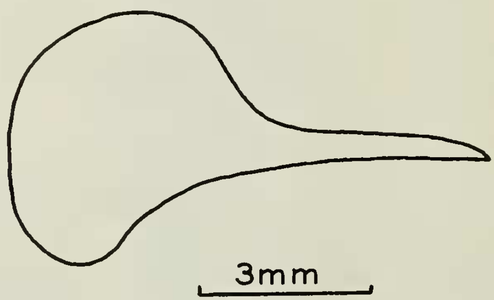

FIG. 13. Maxilla of *Drydenius molyneuxi* (Traquair).

blade than in *D. insignis*. The coronoid bears large stout teeth as in *D. insignis*. The second infraorbital is expanded as in *Pseudogonatodus parvidens* and the infraorbital canal much branched posteriorly as it passes through this bone. There are eleven branchiostegal rays and a median gular.

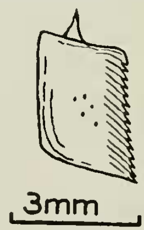

FIG. 14. *Drydenius molyneuxi* (Traquair). Anterior flank scale.

The fins are always poorly preserved. No specimen I have examined shows a pectoral fin, while all that can be said about the anal is that it only possessed a few rays. The pelvics have some seven or eight stout rays and the dorsal about fifteen.

The scales are very large in porportion to body size, at the deepest part of the body numbering between eight and nine rows.

Scale structure. The structure of the scale (Text-fig. 15) is almost identical with that of *Pseudogonatodus macrolepis* (Traquair) even down to the large number of fibres of Sharpey. The bone cells are however larger and considerably fewer in *Drydenius molyneuxi*.

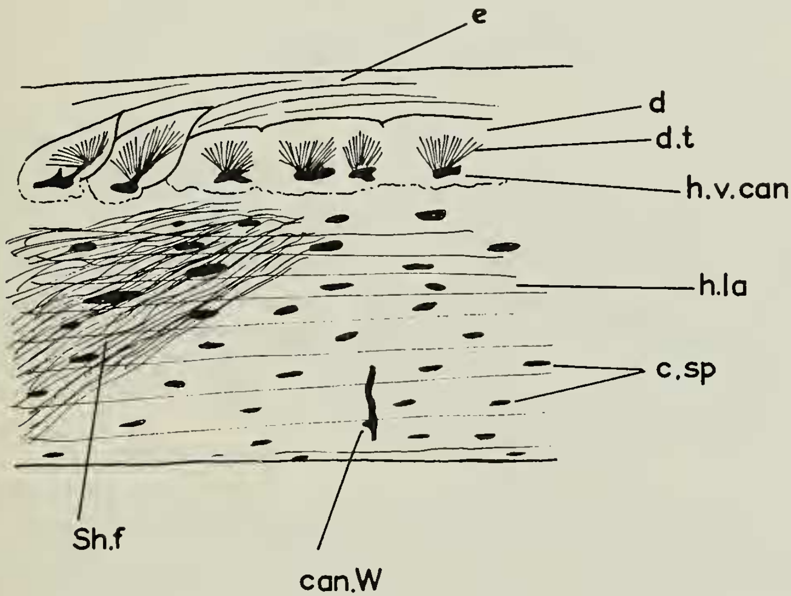

FIG. 15. *Drydenius molyneuxi* (Traquair). Dorso-ventral cross section through mid-lateral scale. ×90. From B.M.N.H. P.7974.

LOCALITY AND HORIZON. The lectotype came from the North Staffordshire Coal Measures (Westphalian C), in the Deep Mine Ironstone at Longton, Staffordshire. It is also recorded from Broadsfield, Fenton. On the Continent it has been recorded from the Upper Carboniferous of France (Pruvost 1919 : 425), Belgium (Pruvost 1930 : 130 ; Heide 1943 : 39) and, doubtfully, from Aachen, Germany (Vangerone 1958 : 472).

Family **TRISSOLEPIDIDAE** Frič 1893

1936 *Gymnoniscidae* Berg : 345.

DIAGNOSIS. Trunk fusiform ; dorsal fin in front of anal fin. Fin rays of all fins relatively few, articulated but not distally bifurcating. Suprascapular large ; suspensorium upright or nearly so ; snout rounded ; teeth prominent on both jaws and branchiostegal rays numerous. Fins with few stout basal fulcra (Woodward 1942) anteriorly (much as in Phanerorhynchidae) but true series of fulcral scales absent.

REMARKS. Frič (1893) erected the Family Trissolepidae to include *Trissolepis* Frič. Unfortunately *Trissolepis* is a synonym of *Sphaerolepis* Frič. This family contains *Sphaerolepis* Frič and *Sceletophorus* Frič from the Upper Carboniferous. The Trissolepididae were probably derived from the earlier Holuridae and as such show some similarity to the Phanerorhynchidae and to the Teleopterinidae which likewise had their origins in the Holuridae. The Family Atherstoniidae nov. (which includes *Atherstonia* Woodward) are also related to the Trissolepididae.

Genus *SPHAEROLEPIS* Frič 1877

1893 *Trissolepis* Frič : 76.

DIAGNOSIS (emended). Trunk fusiform, tail very long ; dorsal fin in front of anal fin, opposite gap between anal and pelvic fins. Dorsal contour arched in advance of dorsal fin ; pectoral fins small, pelvics larger than pectorals. Apart from pelvics all fins have stout basal fulcra (Woodward 1942) forming their leading edges, but true series of fulcral scales absent. All lepidotrichia stout, articulated and not distally bifurcated. Suspensorium upright ; opercular more than three times as deep as subopercular. Dorso-posterior blade of maxilla rounded as in *Pseudogonatodus*. Fossa present in skull roof at junction of parietal, frontal and dermopterotic. Teeth numerous, of moderate size and in one series. Scales cycloidal, those in anterior trunk region being pectinated posteriorly.

TYPE SPECIES. *Sphaerolepis kounoviensis* Frič. The only species.

REMARKS. Frič (1875 : 76) in the first mention of the species *Kounoviensis* merely stated that it belonged to a new genus without erecting a generic name for it. Later in 1877 he placed it in the new genus *Sphaerolepis*. Two years later in his " Fauna der Gaskohle " (1879, **1** : 31) he referred to it as *Sphaerolepis kounoviensis*, but later in the same work (1893, **3**, 2 : 76) changed the name to *Trissolepis kounoviensis* and put it in a new family, the Trissolepidae. Clearly since his original descriptions (1875, 1877) give enough information to recognize the species then the generic name *Sphaerolepis* must stand and *Trissolepis* must be treated as a synonym.

Sphaerolepis kounoviensis Frič

(Plate 1; Text-figs. 16–18)

1875 (Nov. gen.) *Kounoviensis* Frič : 76.
1877 *Sphaerolepis kounoviensis* Frič : 46.
1879 *Sphaerolepis kounoviensis* Frič ; Frič, **1** : 31.
1891 *Sphaerolepis kounoviensis* Frič ; Woodward : 523.
1893 *Trissolepis kounoviensis* (Frič) Frič, **3**, 2 : 76, pls. 109–112, text-figs. 277, 278.
1907 *Sphaerolepis kounoviensis* Frič ; Traquair : 106.
1909 *Sphaerolepis kounoviensis* Frič ; Traquair : 107.
1944 *Trissolepis kounoviensis* (Frič) ; Westoll : 65.

DIAGNOSIS. Fishes not exceeding 11 cm. in total length ; body fusiform, length of head contained almost five times and greatest depth of body just over four times in total body length. Dorsal fin shorter based than anal fin ; two ridge scales in front of dorsal. Fossa present in skull roof at junction of parietal, frontal and dermopterotic.

SYNTYPES. Four specimens in the Národní Museum, Prague, from the Upper Carboniferous of Kounová, Czechoslovakia.

MATERIAL. Photographs and casts of syntypes, and no. 47491 in the British Museum (Natural History).

DESCRIPTION. *The skull.* The bones of the skull and course of the sensory canals are shown in Text-fig. 16. The skull is short and high with an almost vertical suspensorium while the snout is bluntly rounded. The suprascapulars are large, stout and meet in the midline anteriorly. The extrascapular series, consisting of the

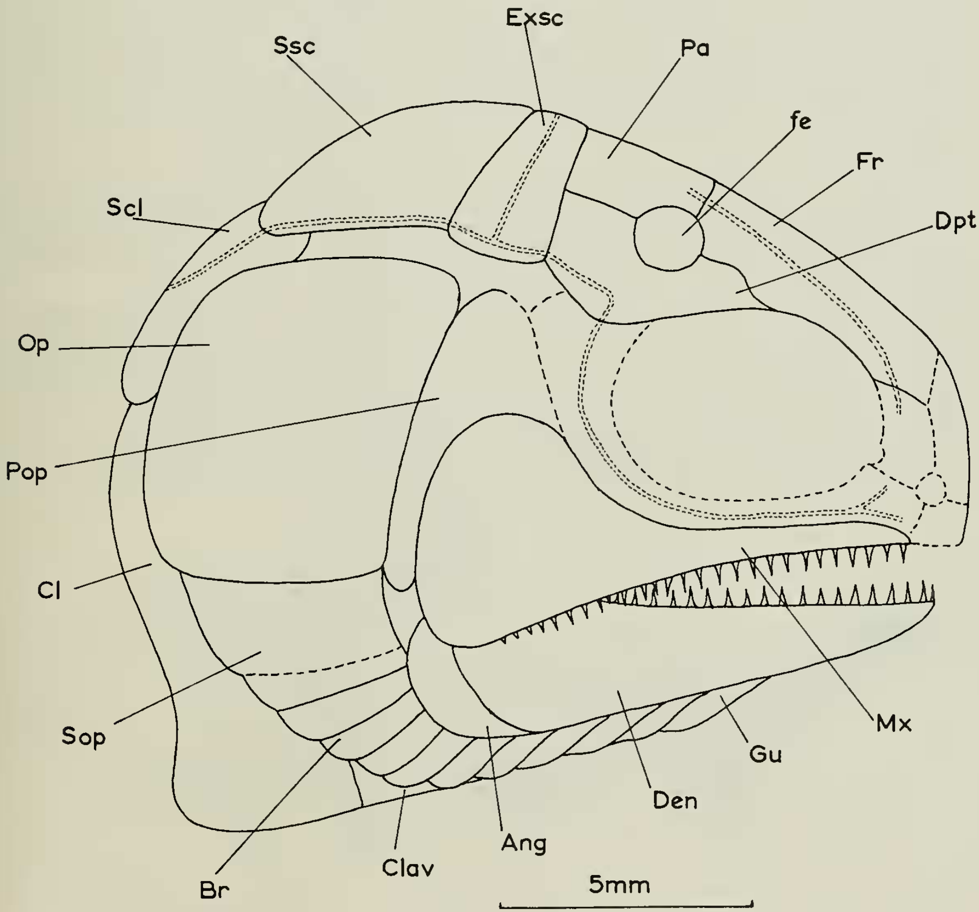

FIG. 16. *Sphaerolepis kounoviensis* Frič. Reconstruction of skull in lateral veiw.

normal single pair of bones, is somewhat larger than in the average palaeoniscoid. The postero-dorsal surface of each extrascapular is peculiarly scalloped. The parietals are almost square while the lateral wall of the skull roof is composed of a short, broad, dermopterotic, but the position and extent of the dermosphenotic is not clear on any of the specimens. Frič (1893, pls. 109–112) in his interpretation of the skull roof indicated a true fossa in the region of the junction between the parietal, frontal and dermopterotic. From a careful study of that region in the specimen concerned I agree with Frič that such a fossa did exist in life and was not caused after death by an otolith as suggested by Westoll (1944 : 65). In this respect *Sphaerolepis* shows some similarity to *Pyritocephalus* Frič (Westoll 1944).

The frontals are large and the nasals and postrostral long, but the remaining bones constituting the snout region could not be distinguished with any degree of certainty although the position of the nares could be seen.

The maxilla is of unusual shape being rounded dorsally as in *Pseudogonatodus* nov. The teeth on the maxilla are of moderate size (somewhat larger than in the normal palaeoniscoid) and arranged in a single series. The preopercular is almost vertical and much narrower than in most palaeoniscoids and in this respect it also resembles *Pseudogonatodus* nov. The opercular is more than three times deeper than broad. Beneath the subopercular are some ten branchiostegal rays with a median gular anteriorly.

Lower jaw. The angular only occupies a small portion of the jaw surface while the dentary is considerably thickened ventrally and forms the major portion of the outer surface of the jaw. A single row of stout teeth is present on the upper margin of the dentary.

The palate. The parasphenoid is short, narrow anteriorly, but expands posteriorly, and in general size and shape is similar to that of *Pteronisculus* White (Nielson 1942). Both the vomers and palatines are large and bear prominent teeth. Those on the palatine are stout, rounded, arranged in a cluster about three deep.

The paired fins and their girdles. The supracleithrum extends about half way down the opercular and the cleithrum is elongated and comparatively stout. A

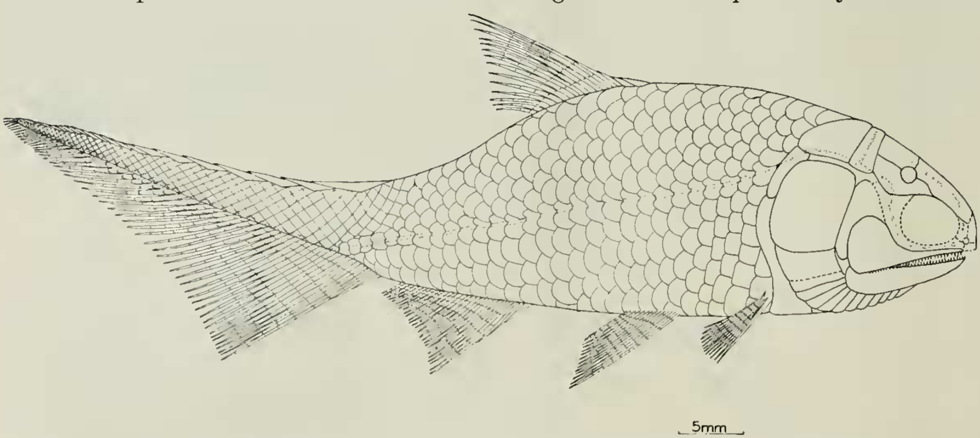

FIG. 17. *Sphaerolepis kounoviensis* Frič. Restoration of whole fish.

distinct ornamentation is visible on both the supracleithrum and the cleithrum, consisting of lines of sharply pointed tubercles that follow the length of the bone. Anteriorly a short clavicle can be seen.

The pectoral fin is small with eleven to thirteen lepidotrichia. Apart from the ray forming the leading edge all the lepidotrichia have distinct articulations.

The pelvic fin is larger with fourteen to sixteen rays, all of them articulated.

The unpaired fins. The dorsal fin is composed of about fifteen stout, articulated lepidotrichia and is preceded by two ridge scales. The anal fin is longer based than the dorsal and is made up of more rays, between twenty-five and twenty-eight. As in the dorsal fin there are two or three basal fulcra (Woodward 1942) in the anal forming a stout leading edge to the fin.

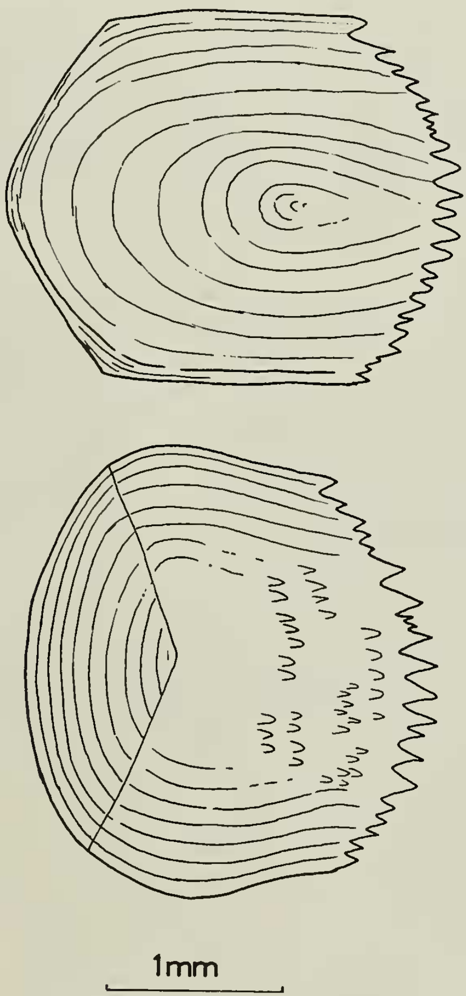

FIG. 18. *Sphaerolepis kounoviensis* Frič. Anterior flank scales.

The caudal fin is heterocercal but not cleft as in most palaeoniscoids, and in this respect *Sphaerolepis* resembles *Phanerorhynchus* Gill, *Palaeoniscinotus* Rohon, *Holurus* Traquair and *Holuropsis* Berg. The rays are all articulated apart from the two stouter ones (basal fulcra) which form the leading edge.

The squamation. The scales, apart from those on the tail, are cycloidal. In this feature *Sphaerolepis* shows some similarity to *Cryphiolepis* Traquair and *Browneichthys* Woodward (Griffith 1958). The exposed surface of the majority of these cycloidal scales is covered with closely-set, fine, concentric ridges of enamel while those in the anterior flank region have a much stronger ornamentation. Thus the first three to four rows of scales behind the pectoral girdle have several rows of backwardly pointing tubercles on the posterior surface and the posterior edge pectinated (Text-fig. 18).

The scales on the caudal body-prolongation are rhombic on the sides and on the dorsal surface form a median row of imbricating, V-shaped scales.

Locality and horizon. All the known specimens came from the " cannel " coal (" gas-coal ") of Kounová, Záboř, Hředl and Kněžoves, which is uppermost Westphalian extending into the lowermost Stephanian (Floral zones H–I).

Genus *SCELETOPHORUS* Frič 1894

1894 *Phanerosteon* Traquair ; Frič : 92 (*errore*).
1936 *Gymnoniscus* Berg : 345.

Diagnosis (emended). Trunk fusiform, tail short ; dorsal fin situated in front of anal fin, opposite gap between anal and pelvic fins. Dorsal contour more or less flat ; pectoral and pelvic fins of about same size, both relatively small. All fins with stout basal fulcra (or spines) forming their leading edges, but true series of fulcral scales absent. All fin rays stout, articulated, but not distally bifurcated. Opercular not quite twice as deep as subopercular. Dorso-posterior blade of maxilla rounded as in *Sphaerolepis*. Teeth numerous, of moderate size, arranged in single series. Scales rhomboidal and, for most part, ornamented with fine, concentric ridges of enamel. Ridge scales prominent along dorsal contour.

Type species. *Sceletophorus biserialis* Frič. The only species.

Remarks. Frič (1894 : 92) also described the new species *Phanerosteon pauper* from the same locality as *Sceletophorus biserialis*. *Phanerosteon pauper* is a small naked form which Frič (1894 : 92) put into Traquair's (1881 : 39) genus *Phanerosteon* even though he thought it possibly the young of *Sceletophorus biserialis*. Later Berg (1936 : 345) erected the new genus *Gymnoniscus* for its reception. Westoll (1944 : 66) believed Frič (1894 : 92) to be right in his suggestion that *Phanerosteon pauper* was probably the young of *Sceletophorus biserialis*, and after a study of the specimen concerned I have no doubt that that is so.

Wade (1935) has already shown in *Brookvalia* that scale development starts behind the pectoral girdle, along the lateral line canal and on the axial lobe of the tail, and this is precisely where scales are to be found on the juvenile form of *Sceletophorus biserialis* Frič. In *Phanerosteon* Traquair and to a certain extent in *Carboveles* White (1927) the development of scales has been arrested at this point and thus they both provide examples of paedomorphosis.

Sceletophorus biserialis Frič

(Plates 2, 3; Text-figs. 19–21)

1894 *Sceletophorus biserialis* Frič, **3**, 3 : 88, pls. 116, 117.
1894 *Phanerosteon pauper* Frič, **3**, 3 : 92, pl. 117.
1912 *Phanerosteon pauper* Frič; Traquair : 168.
1936 *Gymnoniscus pauper* (Frič) Berg : 345.
1944 *Sceletophorus biserialis* Frič; Westoll : 65.
1944 *Phanerosteon pauper* Frič; Westoll : 66.

DIAGNOSIS. Fishes not exceeding 6 cm. in total length, body fusiform, length of head contained just over four times and greatest depth of body just under four times

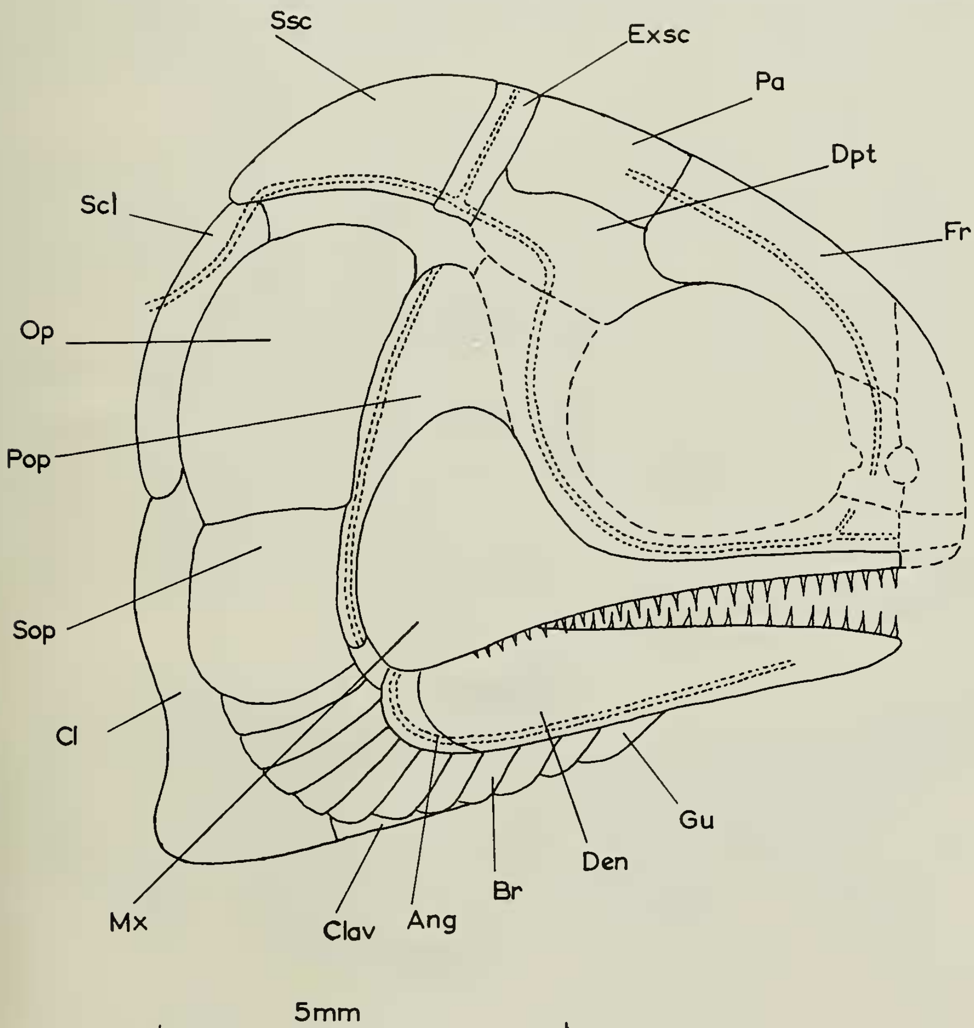

FIG. 19. *Sceletophorus biserialis* Frič. Reconstruction of skull in lateral view.

in total body length. Four ridge scales in front of dorsal fin with paired basal fulcra. Series of large ridge scales running from immediately behind dorsal fin to tip of tail. Single ridge scale in front of anal fin.

SYNTYPES. Both the two syntypes of *Scletophorus biserialis* Frič and the two syntypes of *Phanerosteon pauper* Frič are in the Národní Museum, Prague. All are from the Upper Carboniferous of Třemošná, Czechoslovakia.

MATERIAL. Photographs and casts of syntypes.

DESCRIPTION. *The skull.* The skull is large in comparison to total body length. The suspensorium is vertical and the snout bluntly rounded. The suprascapulars are large and the extrascapulars narrow. In front of the extrascapulars are a pair of large, rectangular parietals which are followed by equally stout frontals. The post-rostral and nasals are long and narrow, but the bones making up the lateral roof of the skull could not be distinguished with any degree of accuracy. However there is no evidence of a fossa in the skull roof as in *Sphaerolepis* Frič.

The maxilla is rounded postero-dorsally much as in *Sphaerolepis* and *Pseudogonatodus*. The teeth on the maxilla are of moderate size, arranged in a single row and similar to those in *Sphaerolepis*. The preopercular is nearly vertical and shaped much as in *Sphaerolepis*. However the opercular is less than twice as deep as the subopercular and considerably deeper than it is broad. Beneath the subopercular are about ten branchiostegal rays with a median gular anteriorly.

The lower jaw. Again very similar to *Sphaerolepis* with the angular only occupying a small portion of the jaw surface and the dentary thickened ventrally. A single row of stout teeth is borne on the upper margin of the dentary.

The axial skeleton. The neural and haemal arches are seen as distinct ossifications (see Pl. 2). The ossified vertebral centra (Wirbelröhre) figured by Frič in *Scletophorus biserialis* (1894, fig. 286) and also in *Phanerosteon pauper* (1894, fig. 287) do not exist: what Frič saw was the lateral line canal of the opposite side of the body, which shows through the body scaling as a segmental, tubular structure, in such a position (due to post mortem twisting of the body) as to be aligned in the gap between the anterior neural and haemal arches (Pl. 2).

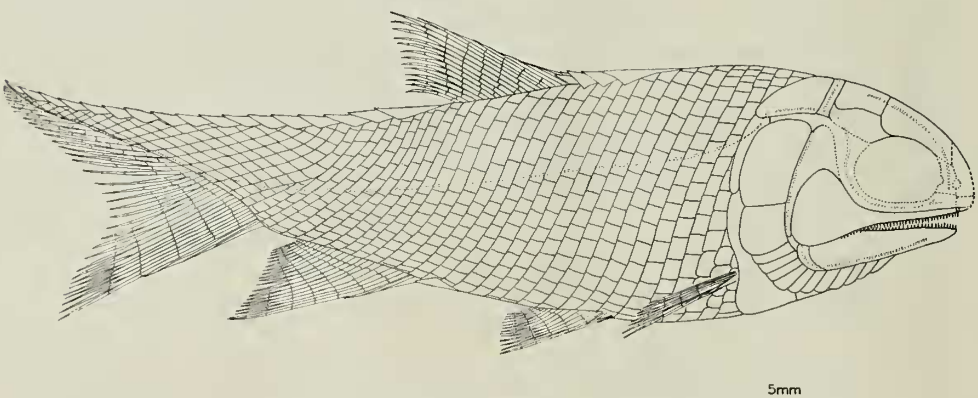

FIG. 20. *Sceletophorus biserialis* Frič. Restoration of whole fish.

The paired fins and their girdles. The supracleithrum is longer than in *Sphaerolepis* and extends over two-thirds of the way down the opercular. The cleithrum is broad and anteriorly united with a short clavicle.

The pectoral fin is longer than the pelvic and composed of only eight rays. Anteriorly the leading edge is made up of three, short, stout unarticulated basal fulcra (Woodward 1942). Frič (1894, pls. 116, 117) in his reconstruction of *Sceletophorus biserialis* figures some sixteen lepidotrichia in the pectoral fin, but again he was misled by the impression of the pectoral fin of the opposite side which shows through the body scaling (Pl. 2).

The pelvic fin contains about thirteen lepidotrichia all of which are stout and articulated. At the leading edge of the fin there are three short, unarticulated basal fulcra.

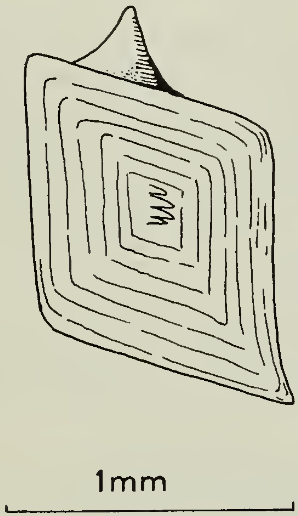

Fig. 21. *Sceletophorus biserialis* Frič. Anterior flank scale.

The unpaired fins. The dorsal fin has between fifteen and seventeen articulated fin rays with the leading edge reinforced by three pairs of unarticulated basal fulcra.

The anal fin is longer with some twenty robust articulated rays. The leading edge is again strengthened by three unarticulated basal fulcra which unlike those in front of the dorsal fin are unpaired.

The caudal fin is heterocercal and only partially cleft, shorter than in *Sphaerolepis*. The rays are stout and articulated and again there are three or four strong, unarticulated basal fulcra preceding it.

The squamation. The scales are rhomboidal and ornamented with fine concentric ridges of enamel, but the scales immediately around the pectoral fin are almost cycloidal while those in the anterior flank region have in addition to the fine concentric ridges of enamel two or three small backwardly directed spines in the mid-scale region.

Locality and horizon. All the known specimens came from the " cannel " coal of Třemošná, which is uppermost Westphalian extending into the lowermost Stephanian (Floral zones H–I).

Family **PHANERORHYNCHIDAE** Stensiö 1932

Diagnosis. As for the genus *Phanerorhynchus*.

Remarks. This family includes the single genus *Phanerorhynchus* Gill. The peculiar nature of its fins suggests a relationship to the Haplolepiformes while the skull could easily have been derived from that of a primitive haplolepid-like form by elongation of the snout region. Like the Haplolepiformes the Phanerorhynchidae were probably derived from the earlier Holuridae. Superficially the Phanerorhynchidae show considerable similarity to the later Chondrosteiformes and Acipenseriformes.

Genus ***PHANERORHYNCHUS*** Gill 1923

Diagnosis. Body fusiform ; dorsal fin almost opposite anal fin, both fins triangular, anal smaller of two, form of caudal fin unknown. Pectoral and pelvic fins small ; all fins with stout, unjointed rays which never bifurcate. Snout drawn out as distinct rostrum projecting well beyond anterior limit of lower jaw. Suspensorium almost vertical, opercular more ovoid than rectangular. Orbit small, dentition feeble or absent. Scales large, dorsal and ventral ridge scales prominent, ridge scales graduating into very stout basal fulcra (Woodward 1942) in front of fins (true fulcral scales absent).

Type species. *Phanerorhynchus armatus* Gill, the only known member of the genus.

Phanerorhynchus armatus Gill

(Text-figs. 22,23)

1915 Imperfectly preserved small fish, Woodward : 73.
1923 *Phanerorhynchus armatus* Gill : 465, text-fig. 1.
1932 *Phanerorhynchus armatus* Gill ; Stensiö : 78, text-fig. 29.
1936 *Phanerorhynchus* Gill ; Berg : 345.
1939 *Phanerorhynchus armatus* Gill ; Moy-Thomas : 118, text-fig. 31*a*.

Diagnosis. Fishes not exceeding 4 cm. in total length, body fusiform, length of head contained slightly more than three times and greatest depth of body three times in total body length. Lepidotrichia stout, smooth, unjointed and not bifurcated. Scales large, median flank row containing lateral line about three times deeper than broad. Only six obvious scale rows. Dorsal ridge scales with stout spines graduating into basal fulcra in front of dorsal fin. Ventral ridge scales prominent but with less obvious spines.

Holotype. Manchester Museum, L.8585, an almost complete specimen, minus tail, in a clay ironstone nodule; the only known specimen of this species. From the Middle Coal Measures of Sparth, Lancashire.

Description. *The skull.* The general shape of the skull can be seen from Text-fig. 22. The anterior end is drawn out into a very distinct rostrum. The suprascapulars are large and are joined to a pair of extrascapulars anteriorly. The parietals

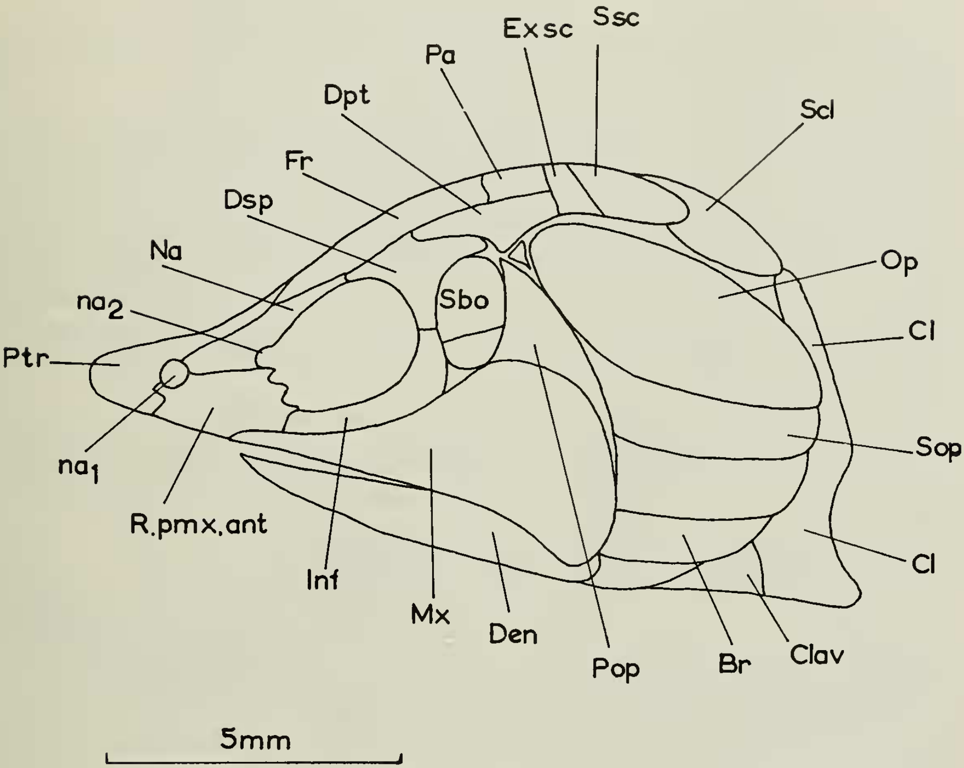

FIG. 22. *Phanerorhynchus armatus* Gill. Reconstruction of skull in lateral view.

are relatively small and square in outline, while the frontals are long with their anterior margins produced into a point thus giving the postrostral a V-shaped insertion between the two frontals. On either side of the single median postrostral is a stout, long, nasal element. The nasal is broad and its lateral margin has an emargination (na_2) which indicates the position of the posterior nostril. The anterior nostril (na_1) lies between the nasal, postrostral and rostro-premaxillo-antorbital. Posteriorly the nasal joins the frontal and the dermosphenotic, anteriorly the rostro-premaxillo-antorbital. The postrostral is only slightly convex transversely in its posterior half, but the anterior half of the bone is strongly curved in a transverse as well as longitudinal direction, giving the head a distinct rostrum. Ventrally the postrostral meets the paired rostro-premaxillo-antorbitals. The rostro-premaxillo-antorbital is notched anterio-dorsally (na_2) while posteriorly it is ornamented with several backwardly pointing short spines. Dorsally it articulates with the nasal and posteriorly with both the maxilla and infraorbital.

The lateral wall of the skull roof comprises two bones, the dermopterotic and the dermosphenotic. The dermopterotic is broad posteriorly but tapers almost to a point anteriorly where it fits between the dermosphenotic and the frontal. The dermosphenotic is larger than the dermopterotic and anteriorly meets the nasal. Ventrally the dermosphenotic abuts against the apparently single, long, curved infraorbital bone. Behind the infraorbital and below and behind the dermosphenotic are two suborbitals, of which the dorsal is by far the larger.

The maxilla is of the normal palaeoniscoid outline, but its anterior prolongation is somewhat short ; it is ornamented with concentric striae of enamel. The pre-opercular is again of the normal palaeoniscoid form and from the inclination of its posterior border the suspensorium can be seen to be almost upright. The opercular is large, ovoid in shape and ornamented with sparse longitudinal ridges of enamel. The subopercular is much smaller and scarcely larger than the succeeding branchiostegal ray. At least four branchiostegal rays can be seen, but whether or not a gular plate is present could not be determined. As already mentioned by Watson (*in* Gill 1923) there appears to be a small triangular plate between the top of the pre-opercular and the dermopterotic.

The lower jaw. The lower jaw is ornamented with longitudinal striae of enamel, but apart from the mandibular sensory canal with its three lateral tubules running

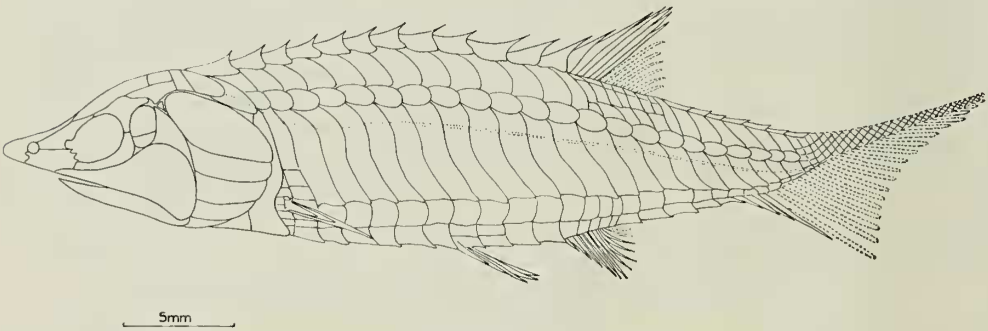

FIG. 23. *Phanerorhynchus armatus* Gill. Restoration of whole fish.

out obliquely towards the surface of the jaw little could be made out. Whether or not teeth were present could not be determined : if present they must have been very small.

The paired fins and their girdles. Of the pectoral girdle, the supracleithrum and cleithrum are ornamented with concentric ridges of enamel which run parallel to the margins, nearer the centre of the bones these ridges give way to tubercles. The supracleithrum and cleithrum are of normal palaeoniscoid proportions and ventrally there is a pair of stout clavicles. Of the pectoral fin, only the base and one fulcral scale are to be seen on the specimen, but probably there were four to eight fin rays. The pelvic fin has a very short base and is composed of four to six rays.

The unpaired fins. Both the dorsal and anal fins are small, situated far back and almost opposite one another, the dorsal being slightly the larger. Of the dorsal fin, some six rays can be seen with certainty but the total number was probably nearer twelve. On the anal fin about nine rays can be counted, but again there may have been one or two more. Only the base of the slender tail shaft is preserved, with two very stout fulcra ventrally, followed by three stout fin rays.

The squamation. The body scales have been somewhat distorted but the true arrangement is given in Text-fig. 23. On each of the largest, middle flank scales there are two distinct tubercles, one near the dorsal edge and the other two-thirds of the way down : the dorsal one represents the passage of the lateral line. The first row of scales beneath the dorsal ridge scales also has a large tubercle near the base of each scale. All these tubercles are long and point posteriorly, often extending beyond the posterior margin of the scale in which they arise.

The dorsal row of ridge scales is composed of single scales, but the ventral row consists of paired scales up to the pelvic fin. After the anal fin the ridge scales are single and unpaired.

Locality and horizon. Sparth, near Rochdale, Lancashire. Middle Coal Measures, Upper Carboniferous, Ammanian (*Anthracoceras* Zone A).

Family **OSORIOICHTHYIDAE** nov.

Diagnosis. Trunk fusiform ; mandibular suspension moderately oblique, pectoral fins with large number of articulated and distally bifurcating rays. Rostrum well developed, teeth arranged in single series. Opercular small, with accessory opercular separating it completely from subopercular, all three bones approximately same size. Branchiostegal rays very numerous, gular large ; scales small and rhomboidal.

Remarks. This family has been erected to include the single genus *Osorioichthys* Casier from the Upper Devonian of Belgium. The condition of the opercular apparatus separates it from all other described genera with the exception of *Rhabdolepis* Troschel (Gardiner 1963). It differs from *Rhabdolepis* in the more primitive arrangement of the skull roof and in the large size of the accessory opercular in relation to the opercular. The Osorioichthyidae represents a specialized side line from the main palaeoniscoid stock.

Family **GYROLEPIDOTIDAE** nov.

Diagnosis. Body fusiform ; dorsal fin arising just anterior to anal fin ; both fins of moderate size ; caudal fin powerful, deeply cleft, equilobate. Paired fins moderate to large. All fins with large, articulated and distally bifurcating rays, and stout fulcra anteriorly. Skull rounded anteriorly without well developed rostrum ; suspensorium only slightly inclined, opercular high and subopercular somewhat reduced ; dermohyal large, but no accessory opercular present. Dermopterotic long, suborbital series well defined, teeth stout and in single series. Large dorsal ridge scales running from occiput to dorsal fin and from dorsal fin to caudal extremity ; large ventral scales extending from anal fin to base of caudal.

Remarks. This family includes *Gyrolepidotus* Rohon and *Palaeobergia* Matveeva from the Lower Carboniferous of Russia. It belongs to a closely related complex of families including the Carbovelidae, Gonatodidae *nov*, Cosmoptychiidae, Acrolepididae, Elonichthyidae, Rhadinichthyidae, Canobiidae, Pygopteridae, Rhabdolepididae, Styracopteridae and Cryphiolepididae. All possess many features in common and were derived from the same stock. The Gyrolepidotidae however can be separated from any one of these families by the stout nature of the fin rays, the very large fulcral scales and the large size of the dermohyal.

Family **AMPHICENTRIDAE** Moy-Thomas 1939 : 115

DIAGNOSIS (emended). Body very deeply fusiform ; dorsal and anal fins triangular and long based, caudal fin heterocercal, inequilobate and deeply cleft : lepidotrichia of all fins jointed and distally bifurcated ; fulcral scales large. Suspensorium almost vertical, orbit small, opercular smaller than subopercular, maxilla triangular and massive. Gular narrow, flank scales deeper than broad ; dentition modified for crushing. Ectopterygoids and coronoids with robust teeth.

REMARKS. This family includes the following genera : *Chirodus* M'Coy, *Cheirodopsis* Traquair, *Eurynothus* Agassiz, *Eurynotoides* Berg, *Paraeurynotus* Chabakov, *Globulodus* Munster, *Protoeurynotus* Moy-Thomas & Dyne and possibly *Tompaichthys* Obruchev. Moy-Thomas (1939 : 115) first recognized that the platysomids could be separated into two distinct families and within the Amphicentridae he included *Amphicentrum* Young, *Protoeurynotus* Moy-Thomas & Dyne, *Eurynotus* Agassiz and *Cheirodopsis* Traquair. However *Amphicentrum* Young 1866 is synonymous with *Chirodus* M'Coy 1848 (Dyne 1939 : 195).

Family **ATHERSTONIIDAE** nov.

DIAGNOSIS. Body fusiform ; dorsal fin arises well in front of anal fin ; both fins triangular. Pectoral and pelvic fins large, anterior rays of pectoral unarticulated proximally. All fins with numerous small fulcra anteriorly and rays closely articulated but *not* distally bifurcated. Skull with moderately developed rostrum and oblique suspensorium. Opercular much larger than subopercular. Scales rhomboidal with pronounced ridges of enamel ; large ridge scales running from occiput to dorsal fin.

REMARKS. The family includes the single genus *Atherstonia* Woodward which ranges from the Upper Permian to the Upper Triassic. The Atherstoniidae are close to the Trissolepididae, particularly in the make-up of the fins in which the rays are not bifurcated distally. They differ from the Trissolepididae in the presence of fulcral scales, in the absence of basal fulcra and in the more oblique suspensorium.

Family **LAWNIIDAE** nov.

DIAGNOSIS. Body fusiform ; dorsal fin large, arising anterior to smaller anal fin ; caudal fin powerful, deeply cleft and inequilobate. Paired fins stout, of moderate size. Lepidotrichia of all fins closely articulated and distally bifurcated ; small fulcral scales present along leading edges of fins. Skull without well-developed rostrum, suspensorium only moderately oblique, opercular and subopercular of approximately same size. Preopercular high, with small dermohyal between it and opercular. Posterior nasal aperture (nostril) completely enclosed posteriorly by antorbital (a specialization not normally seen below holostean grade). Teeth stout and in single series. Ridge scales present in front of unpaired fins.

REMARKS. The Family Lawniidae is used to include a single fresh water genus *Lawnia* Wilson (1953), from the Permian of Texas. In body shape, disposition of fins and scale structure this family resembles both the Amblypteridae and the earlier Gonatodidae, but the specialized arrangement of the snout in the Lawniidae clearly separates it from either of these families.

Family **COSMOLEPIDIDAE** nov.

DIAGNOSIS. Trunk elegantly fusiform ; dorsal and anal fins triangular, with posterior rays very short. Dorsal fin opposed to space between pelvics and anal, caudal fin deeply forked, inequilobate and with upper lobe much attenuated. All fins of moderate or small size with broad, articulated rays, distally bifurcating. Rays of pectoral fins unarticulated proximally, minute fulcra on all fins. Mandibular suspensorium oblique, teeth consisting of inner series of stout conical laniaries and outer series of more numerous smaller teeth. Supraorbital sensory canal unites with infraorbital canal. Scales thick and small.

REMARKS. The Cosmolepididae is another monogeneric family, containing the Lower Liassic *Cosmolepis* Egerton. This family resembles the earlier Palaeoniscidae in general body form, but can be distinguished from it by the greater length of the jaws, the more oblique suspensorium and the structure of the scales. A diagnostic character is that the supraorbital sensory canal unites with the infraorbital canal, a condition seen in only one other chondrostean (*Brookvalia* Wade).

Family **BRACHYDEGMIDAE** nov.

DIAGNOSIS. Skull without pronounced rostrum, suspensorium almost upright, orbit small ; opercular and preopercular of comparable size, preopercular high and with several dermohyals between it and opercular series. Branchiostegal rays numerous and suborbital series present. Maxilla stout, with very large teeth on anterior half. Large teeth in single series on dentary and rostro-premaxillary. Form of body and fins unknown.

REMARKS. This family is used to include the single genus *Brachydegma* Dunkle (1939), from the Texas Permian. The skull is stout and quite unlike that of any other known palaeoniscoid. On the evidence of scale structure and the shape of the preopercular the Brachydegmidae appear to be nearer the Amblypteridae than any other described family.

Family **BOREOSOMIDAE** nov.

DIAGNOSIS. Body fusiform ; dorsal fin arises in advance of pelvics ; anal fin small, remote ; caudal fin heterocercal, moderately to deeply cleft. Lepidotrichia of fins articulated, distally bifurcated ; fulcra present on all fins. Skull with pronounced rostrum, almost upright suspensorium, high preopercular, and both dermohyals and suborbitals present.

Remarks. The family is erected to include the wide-ranging genus *Boreosomus* Stensiö, while *Mesembroniscus* Wade from the Trias of Australia also possibly belongs here. The Boreosomidae show some affinities to the Palaeoniscidae but are distinguishable from the Palaeoniscidae by the more vertical suspensorium, the high preopercular, the shape of the maxilla, the shorter jaws and the anterior postion of the dorsal fin.

Order PELTOPLEURIFORMES

Family **HABROICHTHYIDAE** nov.

Diagnosis. Body fusiform ; dorsal fin arising in front of anal fin, both fins small and triangular. Caudal fin strongly forked and superficially homocercal ; paired fins small. All fins comprise few, stout rays bifurcated distally and (except in caudal) unjointed proximally ; fulcral scales absent. Skull large, suspensorium upright, opercular at least twice as high as subopercular ; maxilla palaeoniscoid in shape, preopercular large, with vertical posterior margin. Dentition feeble, scaling reduced to single row of greatly deepened scales on flank. Posteriorly this scaling terminates in enlarged, symmetrical, semicircular scale.

Remarks. This family is erected to include the single genus *Habroichthys* Brough, which is readily distinguished from the Peltopleuridae by the presence of the single row of greatly deepened scales on the flank.

III. DISCUSSION

Subclass *CHONDROSTEI*

Although the first undoubted members of the class Actinopterygii are found in the Middle Devonian, it seems probable that certain isolated scales recorded from the Lower Devonian (personal observation) may belong to this class. Comparatively rare at first, the actinopterygians flourished, until today they are the most numerous of the vertebrates. The actinopterygians, like the crossopterygians and dipnoans, probably had their origin in salt water (White 1958). However, by the Upper Devonian the actinopterygians were to be found in both freshwater and marine environments and it seems likely that the primitive actinopterygians were tolerant to both salt and freshwater conditions. Only by this assumption can the world-wide distribution of the palaeoniscoids in the Upper Devonian and Lower Carboniferous be explained. By the beginning of the Mesozoic Era the actinopterygians were almost entirely marine and this has been the main centre of their evolution ever since. Today the vast majority of teleosts are marine and of the freshwater forms many have returned secondarily to this environment from salt water (Romer 1945).

For the sake of convenience, the actinopterygians are divided into four groups which are given Subclass status, in ascending order : the Chondrostei, the Holostei, the Halecostomi and the Teleostei. These groups represent grades of evolutionary development rather than natural subdivisions. During the Palaeozoic the evolution of the Actinopterygii consisted of modifications of the original basic chondrostean design and resulted mainly in abortive attempts to reach the holostean level of organization. In the past it has been customary to group all these [abortive] attempts, together with the more successful ones, into the Subclass (or order) " Subholostei " (Brough 1936, 1939), but this has been abandoned since it not only cuts completely across phyletic lines but was based on adaptive characters. The same criticism can be levelled at the Holostei (which include two distinct lineages) but this group, although not a monophyletic one, includes members which at least have all attained the same grade of structural organization.

The Subclass Chondrostei contains all the Palaeozoic actinopterygians (with one late Permian exception) and although still well represented in the early Mesozoic, its members dwindled rapidly in the late Triassic (as they were replaced by the better adapted holosteans to which they had given rise) until today there are some eight degenerate survivors (*Acipenser* Linnaeus, *Huso* Brandt, *Scaphirhynchus* Heckel, *Kessleria* Bogdanon, *Polyodon* Schneider, *Psephurus* Guenther, *Erpetoichthys* Smith and *Polypterus* Lacépède.) from two orders (Acipenseriformes, Polypteriformes).

The Holostei are the characteristic actinopterygians of the Mesozoic ; the earliest member is recorded from the late Permian (Gill 1923*a*) while today there are but two survivors from two distinct orders, the Semionotiformes (*Lepisosteus*) and the Amiiformes (*Amia*).

The Halecostomi enter the fossil record in the early Mesozoic (Rayner 1937 ; Gardiner 1960) and evolved contemporaneously with the Holostei : they disappeared at the end of the Mesozoic, having given rise to the teleosts.

The Teleostei appeared in the Upper Jurassic : the majority of the present day orders can be distinguished in the Upper Cretaceous, while the majority of modern families seem to have arisen in the Eocene or later.

The early actinopterygians are separated from the crossopterygians and dipnoans by their possession of so-called " ganoid scales ". However, these have undergone considerable modification and reduction in the later members, leaving a relatively thin, simple scale. The " ganoid scale " consists of the same three basic units as in the " cosmoid scale ", a basal portion of bone arranged in parallel layers and an upper portion of dentine (cosmine) capped with layers of enamel (ganoine) : separating the two is a spongy layer representing blood vessel plexuses. The central unit of the " ganoid scale " is equivalent to the basic unit of the " cosmoid scale " and the remainder of the scale arises by the deposition in onion-like fashion of concentric layers of all three materials (bone, dentine and enamel) around this central unit. In the light of the " lepidomorial theory " (Jarvik 1960 ; Stensiö 1961) it would appear that the " ganoid scale " is more complex than the " cosmoid " in that units, instead of being added to the edges, arise in complete rings. In other words, the primordia which go to make up the scale have reached a much higher level of fusion in the " ganoid scale ".

In most Mesozoic forms the scales lose the middle dentine layer and the enamel covering becomes thin in many holosteans and halecostomes, disappearing completely in the teleosts, while in some cases the entire scaly covering may be reduced or lost (pycnodonts and some teleosts). Most of these changes are possibly linked with a need of greater flexibility for more efficient swimming.

The " ganoid scale " of the early actinopterygian *Cheirolepis* is very close in structure to the scales of acanthodians (Gross 1947) and it would seem that the actinopterygians and acanthodians were derived from the same ancestral stock.

The actinopterygians, by virtue of several evolutionary bursts, are a large and diverse group and it is not easy to give a comprehensive definition of such a varied assemblage. However they differ from the majority of crossopterygians and dipnoans (with the exception of the coelacanths) in the absence of internal nostrils. Both nostrils are borne high on the face in primitive forms and the two nares of either side are always separated by the supraorbital sensory canal, although in subsequent evolution the two nostrils become confluent (Gardiner 1963). They differ further from the crossopterygians and dipnoans in the arrangement of the sensory canals of the head, the preopercular canal rarely if ever uniting with the postorbital portion of the infraorbital canal as it does in all crossopterygians. Other points of contrast are to be seen in the nature of the paired and unpaired fins. In the actinopterygians the internal skeleton of the unpaired fins is never concentrated into basal plates but normally consists of separate radials. The paired fins primarily do not have the large fleshy lobes seen in the crossopterygians and dipnoans, but instead the entire fin web is supported by long-based, flexible lepidotrichia which do not have the radials concentrated at their bases. In the more advanced teleosts these fins become much narrower at the point of insertion and consequently much more flexible in their movements. There is normally a single dorsal fin in contrast to the two seen in crossopterygians.

The arrangement of the dermal bones of the head in the early actinopterygians is very similar to that seen in the crossopterygians.

Order PALAEONISCIFORMES

The earliest actinopterygians belong to the Order Palaeonisciformes. This order had its beginnings in the Lower Devonian and the first undoubted members are recorded from Middle Devonian freshwater and marine deposits (Guppy, Lindner, Rattigan & Casey 1958). The Palaeonisciformes attained their maximum development during the Carboniferous and Permian when they were the commonest freshwater fishes, while many had also invaded the seas. They were world-wide in distribution during the Palaeozoic Era, being recorded from Great Britain, many parts of Europe, Greenland, Antarctica, Northern Asia, South and East Africa, South and North America and Australia. Of the thirty-nine families so far recognized, twelve survived into the early Mesozoic, but by the Lower Jurassic only three families remained. However, these three families retained the basic palaeoniscoid condition practically unaltered to the last. One of these three is the Family Coccolepididae, containing the single genus *Coccolepis*, which ranges upwards from the Lower Lias (*Coccolepis liassica*) to the Wealden (*Coccolepis macroptera*) and includes the last members of the Palaeonisciformes. The Palaeonisciformes as a group declined rapidly at the close of the Permian, and by the Middle Triassic they had ceased to be a major constituent of the fish fauna. This very rapid decline can be correlated with the advent of more highly evolved groups of chondrosteans (Perleidiformes, Saurichthyiformes, Pholidopleuriformes, etc.) in the early Triassic.

The Palaeonisciformes represent the basal stock of the actinopterygians and from them all the other actinopterygians evolved.

Basically the palaeoniscoids form a closely-knit group, with most of the members very similar in make up. Owing to inaccurate descriptions it has not hitherto been possible to group the palaeoniscoids effectively in families. However, in the light of more recent researches one may at least attempt to group most of the genera with some assurance. Thus the Devonian palaeoniscoids fall into four distinct families—the Cheirolepididae (*Cheirolepis*), the Stegotrachelidae (*Stegotrachelus, Moythomasia,* etc.), the Tegeolepididae (*Tegeolepis*) and the Osorioichthyidae *nov.* (*Osorioichthys*). However, although all these families are fairly generalized, none of them gave rise to any of the other palaeoniscoid families. The most typical palaeoniscoids belong to the families Elonichthyidae, Acrolepididae, Palaeoniscidae and Coccolepididae, and these families belong to the central stem of palaeoniscoid evolution, one which led to ultimate extinction in the Cretaceous. These families illustrate the fundamental palaeoniscoid plan. There are, however, many variations on this theme, and some of these were to give rise to better adapted chondrostean orders in the late Palaeozoic and early Mesozoic. From some of these more advanced chondrostean orders the later holosteans and halecostomes were derived.

After the Lower Trias the occurrence of palaeoniscoids in marine beds is rare and it appears that about the beginning of their decline the palaeoniscoids forsook the seas and entered fresh waters where they had few if any competitors (many of the more advanced chondrosteans such as the redfieldiids also returned to fresh water during the Lower Triassic). By the Middle Trias they are more conspicuous in fresh-water than in marine deposits. In the fresh-water Middle Triassic beds of Australia there are some seven or eight recorded palaeoniscoid genera (Wade 1935), while in similar beds in South Africa and North America several new genera occur (Woodward 1889; Broom 1913; Gardiner 1966).

The Cheirolepididae, containing but the single genus *Cheirolepis* Agassiz, is a fresh-water family (Middle–Upper Devonian), not far removed from the more normal palaeoniscoid condition except in the possession of minute scales which do not overlap and which closely resemble those of the acanthodians. Another such monogeneric family is the Osorioichthyidae *nov.* from the Devonian of Belgium (Casier 1952, 1954), characterized by a large accessory opercular (in this respect it resembles the later Rhabdolepididae). The Tegeolepididae, which range from the Upper Devonian of North America (Newberry 1888) to the Triassic of Australia (Gardiner 1963), have no fulcral scales, unarticulated rays to the pectoral fins, and small thin scales. The remaining Devonian family, the Stegotrachelidae, is known from marine and fresh-water deposits of Middle and Upper Devonian age and continues into the Lower Carboniferous (Gardiner 1963). It is very close to the main palaeoniscoid stem which was to give rise to the majority of the Carboniferous forms but is exceptional in possessing a pineal foramen. All these four families which arose in the Devonian are end lines independently derived from some hitherto as yet unknown ancestor(s). On the other hand the bulk of the Lower Carboniferous palaeoniscoids form a closely related complex consisting of some twelve families. These are the Carbovelidae, Gonatodidae nov., Gyrolepidotidae nov., Cosmoptychiidae, Acrolepididae, Elonichthyidae, Rhadinichthyidae, Canobiidae, Pygopteridae, Rhabdolepididae, Styracopteridae, and Cryphiolepididae. All possess many features in common and were clearly derived from the same basal stock (one not far removed from the Stegotrachelidae). They all closely adhere to the typical palaeoniscoid condition. From this complex a further thirteen families were subsequently derived—the Brachydegmidae *nov*, Coccocephalichthyidae, Boreolepididae, Boreosomidae *nov*, Palaeoniscidae, Centrolepididae, Coccolepididae, Cosmolepididae *nov*, Amblypteridae, Commentryidae, Dicellopygidae, Aeduellidae and Lawniidae *nov*.

The Brachydegmidae *nov*, Boreolepididae and Coccocephalichthyidae are all too poorly known to establish relationships.

The Palaeoniscidae, Boreosomidae *nov*, Cosmolepididae *nov*, and Centrolepididae all stemmed from an ancestor not too far removed from the Acrolepididae while the Coccolepididae was probably derived from the Palaeoniscidae.

The Amblypteridae, Aedullidae, Commentryidae, Dicellopygidae and Lawniidae *nov* are all related to the Gonatodidae.

The Family Palaeoniscidae includes some ten genera, ranging in time from the Upper Permian to the Upper Trias, and all of which retain the basic palaeoniscoid condition. They are typically fusiform fishes with strongly heterocercal tails, rhomboidal, enamel-covered scales and an oblique suspensorium. The earliest genus is *Palaeoniscum* Blainville (Westoll *in* Aldinger 1937) which ranges from the Upper Permian to the Lower Trias. *Pteronisculus* White (Nielsen 1942) from the Lower Trias of Madagascar, Spitsbergen and Greenland is another typical member, while some of the freshwater palaeoniscoids recorded from the Middle Trias of Australia, such as *Agecephalichthys* Wade, *Myriolepis* Egerton and *Belichthys* Wade (Wade 1935), are also included tentatively in this family. The Palaeoniscidae are close to both the Elonichthyidae and the Acrolepididae, and represent a very conservative stock. The body form, fins and scaling are essentially similar in all three families. The Palaeoniscidae, however, differ from the Elonichthyidae in the development of the cranial roofing bones, in the dorso-anterior development of the preopercular, the enlargement of the suborbital series, the lengthening of the jaws and in the structure of the scales (Aldinger 1937). The Palaeoniscidae differ from the Acrolepididae in the development of the cranial roofing bones, in the more ventral position of the nares, in the greater fragmentation of the infraorbital and suborbital series and in the structure of the scales (Aldinger 1937). Of the two families Elonichthyidae and Acrolepididae, probably the Acrolepididae gave rise to the Palaeoniscidae.

The Centrolepididae contains a single genus *Centrolepis* Egerton which is confined to the marine Lower Lias (Gardiner 1960). It is a fusiform fish with an elongate body, and the fins are of the normal palaeoniscoid pattern with the dorsal opposed to the space between the pelvics and anal. The scales are thick, enamelled and highly ornamented, the suspensorium very oblique and the rostrum pronounced. Apart from the absence of a dermohyal the skull is not dissimilar to that of *Rhadinichthys* or *Palaeoniscum*. In most respects this family has retained the conservative palaeoniscoid structure to the last. It arose from the same stock that gave rise to the Palaeoniscidae but itself gave rise to no other forms.

The Cosmolepididae *nov* is another Lower Liassic marine family, with but one

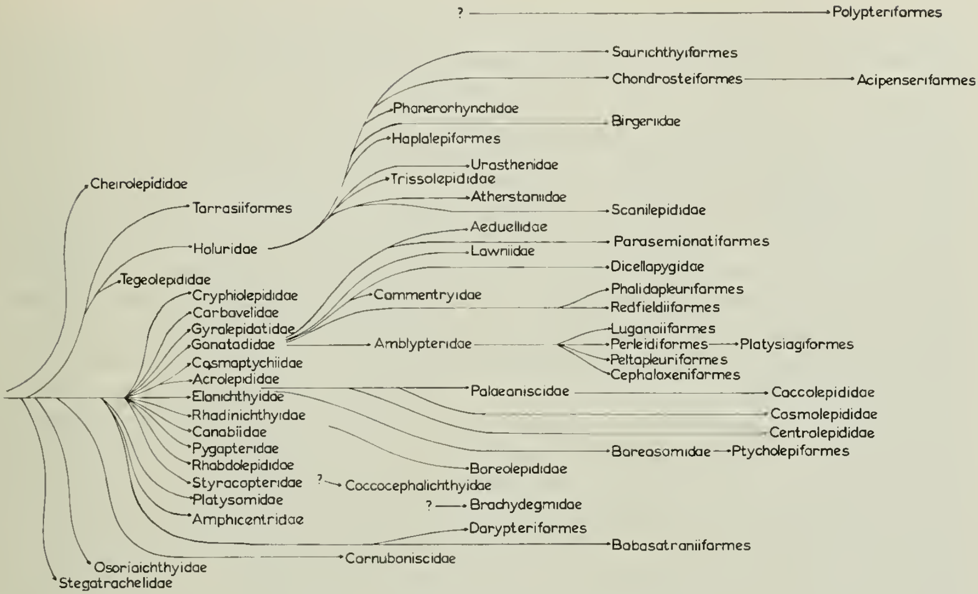

FIG. 24. Phylogeny of the Chondrostei.

representative, *Cosmolepis* Egerton. One of the characteristics of *Cosmolepis* is that the supraorbital sensory canal posteriorly does not enter the parietal but unites with the infraorbital canal (Watson 1925) (a similar condition is seen in *Brookvalia* Wade, *Acentrophorus* Gill and teleosts). The body is elongate, the dorsal and anal fins long-based and the scales small. It differs from the Palaeoniscidae in the greater length of its jaws and suprascapular, the more oblique suspensorium and the scale structure (Gardiner 1960). In general this family is close to *Palaeoniscum* and, like the Centrolepididae, shared a common ancestor with the Palaeoniscidae.

Finally the Family Coccolepididae (Berg 1940) which ranges from the Lower Lias to the Wealden comprises a single genus *Coccolepis*. The coccolepids are slender fusiform fishes with heterocercal tails, deeply forked in most forms but inequilobate. The suspensorium is very oblique, the scales are thin and deeply imbricating but the overhanging rostrum has been reduced and lost and there is no suborbital series present (Gardiner 1960). *Coccolepis* is very similar to the earlier Palaeoniscidae but differs in the absence of a suborbital series and in the more rounded outline of the opercular series. It was directly derived from the Palaeoniscidae.

These last three families all represent end lines which managed to survive comparatively unchanged from the Palaeozoic and which eventually gave way to the far better adapted holosteans.

The Family Boreosomidae *nov* ranges from the Permian to the Middle Trias (Gardiner 1966*a*). The suspensorium is almost vertical but there is still a pronounced rostrum (Lehman 1952). The tail is strongly forked and the dorsal fin is situated well forward with its anterior border in front of the pelvics ; the orbit is large. *Boreosomus* Stensiö itself was an active midwater to surface swimmer, presumably plankton feeding. The affinities of this family are not at all clear, although it seems possible that it is distantly related to the Palaeoniscidae and probably had its origin in the Acrolepididae. However, what is more certain is what the family gave rise to; Brough (1939) has clearly demonstrated the affinities of the family to the Ptycholepiformes, and there can be little doubt that this later chondrostean order was derived from the Boreosomidae.

The Amblypteridae contains four genera ranging from the Upper Carboniferous to the Lower Permian. Its members are characterized by the large paired fins, upright suspensorium and the single series of teeth in the jaws (Gardiner 1963). The family is derived from the earlier Gonatodidae *nov*. The Amblypteridae have many features in common with the earlier Gonatodidae, in particular the height of the preopercular, the straightening of the suspensorium and the single series of teeth in the jaws. The Amblypteridae differ from the Gonatodidae in that the suspensorium is nearer the vertical, the branchiostegal rays are fewer in number and the head is somewhat deeper. Within the Gonatodidae the genera *Pseudogonatodus* nov. and *Drydenius* Traquair show how the maxilla has grown down around the peg-like teeth, and so lead on to the condition seen in the later genus *Paramblypterus* Sauvage (Amblypteridae) where the maxilla almost encases the teeth. A similar sheathing of the teeth is to be seen in *Aeduella* Westoll (Blot & Heyler 1963) which adds weight to the conclusion that the Aeduellidae were also derived from the Gonatodidae.

The Family Aeduellidae is made up of but two genera, *Aeduella* and *Westollia* White & Moy-Thomas, both from the marine Permian. Both are characterized by an upright, narrow preopercular and a maxilla which has no posterior expanded blade (Westoll 1937). The Aeduellidae resemble the earlier Gonatodidae in body shape, disposition and make-up of the fins, and in the possession of a high preopercular. The Aeduellidae differs from the Gonatodidae in that the suspensorium is inclined forward, in the absence of a suborbital series (although anamestic fragmentation of the preopercular is occurring) and in the reduction of the posterior blade of the maxilla.

The Commentryidae (Gardiner 1963) with its single genus has a more typical palaeoniscoid dentition with a double tooth series including an outer row of larger teeth (Blot 1963). There are several parietal ossifications present and the dorsal fin is situated far back with the anal fin more anteriorly placed. This family, like the Amblypteridae, stemmed from the Gonatodidae. The Commentryidae differ from the Gonatodidae in the more posterior insertion of the dorsal fin, in the fragmentation of the parietals and extrascapulars, and in the possession of a double tooth series.

Close to the Commentryidae is another monogeneric family, the Dicellopygidae, from the fresh-water Lower Trias of Bekker's Kraal, South Africa (Brough 1931). The suspensorium is nearer the vertical and the caudal fin strongly forked and almost equilobate, but the general make-up of the skull is comparable to that of the Commentryidae. The scales are relatively large but the maxilla and cheeks are typically palaeoniscoid. This family represents a fresh-water side line.

From fresh-water deposits of Permian age in North America comes yet another monogeneric family, the Lawniidae *nov* (Wilson 1953). In general *Lawnia* resembles the Amblypteridae, apart from the rather specialized arrangement of its antorbital in relation to the narial opening and in body shape (which is fusiform). However there can be little doubt that this family has been independently derived from the earlier Gonatodidae.

Returning now to the closely related complex of twelve families in the Lower Carboniferous, there are two other families, the Amphicentridae and the Platysomidae (Moy-Thomas 1939) which are not so very far removed from this complex and which unquestionably shared a common ancestry with it. These two families include all the deep bodied palaeoniscoids, from the Lower Carboniferous up to the Triassic.

In all essential features the Amphicentridae and Platysomidae are almost identical with the palaeoniscoids making up this related complex of twelve families, but differ mainly in their body shape. The body is laterally compressed and dorso-ventrally deepened. The differences between these two families and the other palaeoniscoids are merely a question of modification as a result of a change in body shape. The most obvious differences are the shape of the maxilla which is almost triangular, the jaw suspension which is vertical (as in the families Canobiidae, Amblypteridae, Aeduellidae, etc.), the short, deep skull and the elongation of the body scales in the dorso-ventral plane. With the change in slope of the face, the nostrils are borne much higher up than in most palaeoniscoids. The dorsal fin is often considerably elongated, while the heterocercal tail is equilobate in many forms, superficially resembling the homocercal condition seen in more advanced actinopterygians. These two families undoubtedly arose from the same parental palaeoniscoid stock and, although their members flourished throughout the Carboniferous and Permian, only one or maybe two genera survived into the Mesozoic (*Caurichthys* Broom, *Platysomus* Agassiz). The two families are separated mainly on the form of the dentition. The Platysomidae have small, conical, often pointed teeth while the Amphicentridae have a more powerful crushing dentition with tooth plates developed on the coronoids and endopterygoids (Dyne 1939). The Amphicentridae did not survive the Palaeozoic, but the Platysomidae are represented in the Lower Trias by *Caurichthys* and also possibly by the long ranging *Platysomus*. Both families were adapted for browsing among the lagoonal coral reefs and finally succumbed to the rather more highly evolved bobasatranids. It seems probable that the bobasatranids, with their more powerful crushing dentition, came from the same basal stock as the Amphicentridae, while both the Amphicentridae and the Platysomidae were derived from the same ancestral stock which gave rise to the related complex of twelve families.

An important Carboniferous family which has been independently derived from the ancestral palaeoniscoid stock is the Holuridae (Moy-Thomas 1939). In this family the bones of the skull conform to the normal palaeoniscoid condition, but it is in the make-up of the fins that the Holuridae differ markedly from all the other palaeoniscoid lineages. The lepidotrichia of all the fins are articulated but *not* distally bifurcating and there are *no* fulcra present. Further the caudal fin is *not* cleft. The Holuridae gave rise to the Phanerorhynchidae, Birgeriidae, Trissolepididae, Atherstoniidae *nov*, and possibly the Urosthenidae and Scanilepididae, while the later chondrostean orders, Haplolepiformes, Saurichthyiformes and Chondrosteiformes also came of this lineage.

The Phanerorhynchidae are known from a single genus, *Phanerorhynchus* Gill from the Upper Carboniferous (Gill 1923). The skull is much as in the more typical palaeoniscoids, apart from the snout which is drawn out into a distinct rostrum projecting beyond the anterior limits of the lower jaw. The actual arrangement of the snout bones is almost identical to that seen in the Haplolepiformes (Westoll 1944). The body scaling is peculiar and consists of very large scales with prominent ridge scales along the dorsal contour, as in the Holuridae. The fin rays are unarticulated and never bifurcated and there are no fulcral scales (as in the Holuridae). The tail was probably not cleft. This family is not far removed from either the Haplolepiformes or the Chondrosteiformes.

The Family Birgeriidae also contains only one recorded genus, *Birgeria* Stensiö which occurs throughout the marine Trias. It is characterized by the large number of suborbitals in the cheek region (Nielsen 1949). The opercular is triangular, the subopercular splint-like and similar to the succeeding branchiostegal rays. The suspensorium is very oblique. The anterior fin rays are not bifurcated and fulcral scales are absent. Like the Phanerorhynchidae it was derived from the holurid lineage.

The Trissolepididae is composed of two genera—*Sphaerolepis* Frič and *Sceletophorus* Frič, both from the Upper Carboniferous of Czechoslovakia. The suspensorium is upright and the snout rounded. The fin rays of all the fins are relatively few in number, articulated but not bifurcating distally. Fulcral scales are absent and the caudal fin is not truly cleft. The Trissolepididae in all these points resemble the earlier Holuridae from which they were derived.

The Family Atherstoniidae *nov* has been erected to include the genus *Atherstonia* Woodward (Upper Permian–Upper Trias). The fin rays in this family are very numerous, articulated but not distally bifurcating. The family is close to the Trissolepididae.

The Scanilepididae are a Triassic family, characterized by a very long dorsal fin containing seventy rays or more (Aldinger 1937). The skull is typically palaeoniscoid, the suspensorium oblique and it may be related to the earlier Holuridae.

Finally the remaining family of this lineage, the Urosthenidae (Woodward 1931), containing the single genus *Urosthenes* Dana, comes from the Permian of New South Wales. The fins have no fulcral scales but it would appear that some of the rays are bifurcated. The absence of dorsal ridge scales on the tail and the peculiar lobed nature of the unpaired fins make the systematic position of this family exceedingly doubtful.

There is one final palaeoniscoid family which has not as yet been dealt with, the Cornuboniscidae (White 1939), containing the single genus *Cornuboniscus* White from the Upper Carboniferous of Cornwall. The genus is characterized by the large maxillae which meet anteriorly and by the reduced opercular and preopercular. Since it does not appear to be related to any of the families described above, an independent derivation from the ancestral palaeoniscoid stock must be postulated.

Leaving the Palaeonisciformes we move on to more advanced Chondrostean orders which have been derived from them.

Order TARRASIIFORMES

The Order Tarrasiiformes includes a single family, the Tarrasiidae, which has only two genera, *Tarrasius* Traquair from the Lower Carboniferous of Scotland and *Palaeophichthys* Eastman from the Upper Carboniferous of Illinois.

The skull in *Tarrasius* is identical with that seen in some of the more primitive Palaeonisciformes (Moy-Thomas & Dyne 1938), while the scales (which are confined to the posterior region) are similar to those of *Cheirolepis* Agassiz (Moy-Thomas & Dyne 1938). However the body is elongated and resembles that of the recent *Polypterus* Lacépède as do the rounded, fleshy lobed, pectoral fins. The dorsal and anal fins are continuous with the caudal which is diphycercal. The fins have no fulcral scales and the rays are articulated but not distally bifurcated ; in these respects the Tarrasiiformes resemble the Holuridae. The Tarrasiiformes are related to the palaeonisciform family Holuridae and must have shared a common ancestry with that family.

Order HAPLOLEPIFORMES

Again this order is composed of a single family, the Teleopterinidae (Berg 1936, Westoll 1944), from the Upper Carboniferous of Europe and North America.

The order is characterized by the structure of the fins in which the lepidotrichia are stout, few in number and not distally bifurcated. Rather peculiar, large, fulcral scales fringe the fins anteriorly, the cleithrum is considerably expanded ventrally, the opercular apparatus is small, the branchiostegal rays are reduced, and the gulars much expanded. The head is broad and short, and anamestic fragmentation of the preopercular is taking place. From a comparison of the snout and fins it seems clear that the Haplolepiformes are fairly close to the Palaeoniscoid family Phanerorhynchidae and as such were derived from the earlier Holuridae.

Order SAURICHTHYIFORMES

This order was founded (Lehman *in* Grassé 1958) on the single family Belonorhynchidae which contains two genera, *Saurichthys* Agassiz, in which all Triassic forms are placed, and *Saurorhynchus* Reis which contains only two species, both from the Lias.

Saurichthys is a widely occurring genus found in the marine Lower Trias of Spitsbergen, Greenland, Madagascar, Europe and North America and in the fresh water Middle Triassic deposits of Australia. *Saurorhynchus* occurs in the marine Lower and Upper Lias of Europe.

These fishes range in size from a few inches to several feet and are elongate, slender forms with a much produced rostrum (Stensiö 1925 ; Gardiner 1960). The tail is abbreviate-diphycercal and the dorsal fin is situated far back, above the anal. The lepidotrichia exceed the endoskeletal supports in number and long slender ribs are present. Fulcral scales are minute or absent. The squamation is not continuous, usually only four rows of scales are present, one dorsal, one ventral and one lateral on either side supporting the lateral line, otherwise the body is naked [*Saurorhynchus brevirostris* (Woodward)]. The maxilla is typically palaeoniscoid, firmly attached to the preopercular and quadratojugal, and from within to the ectopterygoid and dermopalatine. The suspensorium is almost upright, and the opercular apparatus consists of a single large opercular, the branchiostegal rays being reduced to one or completely wanting. The dentition consists of well-spaced, large, conical teeth, with numerous intervening smaller teeth. These well-armed, extremely long jaws mark the saurichthyids as among the most predaceous of the Triassic actinopterygians. The neurocranium is completely ossified but lacks a basipterygoid proces (Gardiner 1960). The sensory canal system is essentially palaeoniscoid and the nasal bone contains two nasal orifices between which the supraorbital sensory canal passes.

The Saurichthyiformes form a degenerating series, closely related both to the Palaeonisciformes and to the Chondrosteiformes, and like the Chondrosteiformes they are not far removed from the earlier Phanerorhynchidae. *Phanerorhynchus* with its small fins, reduced number of scale rows and pronounced rostrum shows the way by which the Saurichthyiformes could have been derived from the Palaeonisciformes. The Saurichthyiformes although successful in the Triassic, never gave rise to any further forms.

Order CHONDROSTEIFORMES

The Chondrosteiformes, like the Saurichthyiformes, appeared in the Lower Trias [*Errolichthys* (Lehman 1952)] and died out in the Upper Jurassic (Liu & Zhou 1964). However, they appear to have been restricted to a purely marine habitat. The Chondrosteiformes show reduction in both body scaling and skull bones. The scaling is rudimentary and the pectoral fin is devoid of fulcral scales and without articulations. The rostrum is moderately to well developed. The maxilla and opercular bones are reduced, the suspensorium still somewhat backwardly inclined and the suprascapular is much elongated. The tail is heterocercal with a well developed scaly lobe. The unpaired fins are typically palaeoniscoid, the rays more numerous than their supports. The best-known member is *Chondrosteus* Egerton from the Lias of Europe. In this form the mouth is withdrawn behind the projecting rostrum and was probably suctorial as in the Recent sturgeons.

The Chondrosteiformes, like the Saurichthyiformes, were probably derived from the earlier Holuridae (possibly *via* the Phanerorhynchidae) but unlike the Saurichthyiformes they went on to give rise to more recent groups. The Acipenseriformes were derived from the Chondrosteiformes.

Order ACIPENSERIFORMES

The Order Acipenseriformes includes two distinct families, the Acipenseridae and the Polyodontidae. Both these families first occurred in the Upper Cretaceous and are represented today by several genera.

The Family Acipenseridae (sturgeons) is widespread today in both salt and fresh water. The best-known genus is *Acipenser* Linnaeus which is first found in marine, Upper Cretaceous deposits. Reduction in ossification has continued from the condition seen in the Chondrosteiformes until little or no ossification of the internal skeleton remains. The scales, as in the Saurichthyiformes, have been reduced to a few rows of large bony scutes, but the fins are still essentially palaeoniscoid in structure and the tail is heterocercal. *Acipenser* is a bottom feeding scavenger, picking up molluscs, crustaceans, etc.

The Family Polyodontidae or paddle fishes first occurred in the Upper Cretaceous of Montana [*Palaeopsephurus* MacAlpin (1947)]. Today members are found in river systems in North America and China (*Polyodon* Schneider and *Psephurus* Guenther respectively). In this family the rostrum has become very elongated and tactile. The eyes are small and above the anterior end of the upper jaw. The primary jaws are very large and the hyomandibular oblique. The opercular has been lost and the subopercular, still large in *Palaeopsephurus*, is much reduced in the living *Polyodon*. The tail is heterocercal and the unpaired fins much as in the Acipenseridae. The skull bones and body scaling are much reduced. As already stated, this order was derived from the earlier Chondrosteiformes.

Order POLYPTERIFORMES

This order is only known from two Recent genera, *Polypterus* Lacépède and *Erpetoichthys* Smith which are confined to the rivers and swamps of tropical Africa.

It has been fashionable of recent years (Lehman *in* Grassé 1958) to separate the Polypteriformes from the Chondrostei and place them in their own Subclass, the Brachiopterygii. However, they retain so many obviously palaeoniscoid features that I do not consider this justified. The scales are typically " ganoid ", the sensory canal system is much as in the higher chondrosteans, and in some respects as in the holosteans. The preopercular is still very much palaeoniscoid in make-up, although its intimate connection with the maxilla has been lost. The snout is primitive and the large number of individual bones above the preopercular is yet another chondostrean character. *Polypterus* shows many discrepancies from the normal chondrostean pattern, especially in the nature of the pectoral fins, the dorsal fins and the tail, but the chondrostean *Tarrasius* from the Lower Carboniferous possesses a continuous dorsal fin and a diphycercal tail. *Polypterus* is merely a much modified chondrostean survivor for which, unfortunately, the connecting links are as yet missing.

Order PERLEIDIFORMES

The Perleidiformes represent a big step forward in chondrostean evolution, and in many respects resemble the contemporaneous holosteans. They were a very successful order, containing some twenty-two or more genera from three families. The earliest members are recorded from the Lower Triassic and after a brief but interesting history the order died out at the end of the Trias due to increasingly unsuccessful competition with the more advanced holosteans.

The origins of this order are somewhat uncertain although it would seem that it was derived from the Amblypteridae. Like the Amblypteridae the Perleidiformes have a high preopercular, which in both *Paramblypterus* and *Perleidus* (Stensiö 1921) shows anemestic fragmentation dorsally. The Perleidiformes still possess typically " ganoid " scales but the general structure of the more advanced members is much closer to the holostean than to the palaeoniscoid condition. The heterocercal tail is modified to a hemiheterocercal condition while the lepidotrichia of the unpaired fins come to equal their endoskeletal supports in number.

The Family Colobodontidae (Stensiö 1916) was essentially a marine one, but with a few fresh-water members. In this family the lepidotrichia of the unpaired fins equal the endoskeletal supports in number and are only articulated distally, the proximal portion being entire. The rays are stiff and bifurcated distally. The fins closely resemble those of holosteans. The suspensorium is upright and the preopercular high and large. *Colobodus* Agassiz from the Middle to Upper Trias was a large, marine form, reaching a length of between two and three feet, and probably a bottom dweller like the present day Cod. Its dentition consists of partly pointed and partly crushing teeth, and this type of dentition marks it off sharply from the Redfieldiiformes. *Perleidus* Deecke ranges throughout the marine Trias and is a more typical member of this family, while *Dollopterus* Abel, *Thoracopterus* Broom, *Gigantopterus* Abel and *Albertonia* Gardiner (1966) on the other hand, all possess enlarged pectoral fins, suggestive of the modern teleostean flying fishes.

The Family Aetheodontidae (Brough 1939) shows some similarity to the Colobodontidae, especially in the form of the dentition, the skull roof, opercular apparatus and preopercular, and it would appear logical to include it here in the Perleidiformes. There is a single genus *Aetheodontus* Brough which occurs in the marine Middle to Upper Trias (Brough 1939). The suspensorium is vertical, the dorsal and pelvic fins remote and the rays few in number. The tail is hemiheterocercal with a short scaly lobe, and the scales are small, stout and numerous.

Finally the Family Cleithrolepididae which is both marine and fresh-water and confined to the Trias. Members are recorded from the Lower Trias of Australia, the Middle Trias of South Africa, the Middle and Upper Trias of Germany and the Upper Trias of England. The fins are much as in the colobodontids except that in the anterior portion of the dorsal fin in *Cleithrolepidina* Berg the lepidotrichia outnumber their supports (Brough 1931). The chief characteristics of this family are the very much deepened form of the trunk and the weak mandible which bears minute teeth. The opercular is smaller than the subopercular, the suspensorium is upright and the preopercular is high, similar to that of some colobodontids (*Meidiichthys* Brough). The family retains some palaeoniscoid characters in common with the Colobodontidae and in the present state of knowledge can most usefully be associated with the Colobodontidae and the Aetheodontidae in the order Perleidiformes.

Order PELTOPLEURIFORMES

This order shows some points of similarity to the Colobodontidae (cf. *Meridensia* Stensiö (1921)) and clearly came from the same ancestral stock. Both *Peltopleurus* Kner and *Meridensia* have a similar body shape, almost identical fins and comparable skulls. *Peltopleurus* differs in the great elongation of its flank scales and in the make up of the snout (Brough 1939). The order contains two families, both of which are confined to the marine Upper Trias. Its members are small fishes with an upright suspensorium, large orbits and a hemiheterocercal tail. The tail is strongly forked, almost symmetrical externally, and with a reduced scaly lobe. The unpaired fins are small with relatively few rays and the rays are unjoined proximally (apart from the caudal) but distally bifurcated. The bones of the head are essentially palaeoniscoid, particularly the maxilla, but the suspensorium is upright. The opercular is large and the preopercular is high and shows anamestic fragmentation, as in the Colobodontidae. The dentition is weak, the scales few in number and those of the flank greatly elongated dorso-ventrally as in the Cephaloxeniformes.

The Family Peltopleuridae (Brough 1939) contains two genera, *Peltopleurus* and *Placopleurus* Brough from the Upper Trias of Besano. These were probably plankton feeders, since their teeth are minute.

The Family Habriochthyidae *nov.* has only one genus *Habroichthys* Brough (1939) and this also comes from the Upper Trias of Besano. *Habriochthys* differs from the Peltopleuridae in having but a single row of greatly deepened scales on the flank, while the tail looks completely homocercal. Further the scaling posteriorly finishes in an enlarged, symmetrical, semicircular scale.

Order CEPHALOXENIFORMES

This order contains one family, the Cephaloxenidae with but a single genus, *Cephaloxenus* Brough, which ranges from the marine Middle to Upper Trias (Brough 1939).

Cephaloxenus is a small fish of deeply fusiform shape and with massive, thick skull bones The fins have relatively few, stiff rays, which are large and unarticulated but distally bifurcated. The suspensorium is slightly inclined backwards, the opercular large and the subopercular small. The tail is hemiheterocercal and almost symmetrical externally, with the scaly lobe reduced. The scales are stout, few in number, those of the flank being greatly elongated dorso-ventrally. The preopercular, although not large, is still high, but the maxilla is rounded posteriorly and relatively broad anteriorly and the orbit is small. The deepened body, large fins, heavily armoured head and crushing dentition shows *Cephaloxenus* to have been a bottom dweller, presumably feeding on molluscs, crustaceans, etc. The affinities of this order remain obscure, but in general body form and elongation of the flank scales there is some similarity to the previous order.

Order LUGANOIIFORMES

The Order Luganoiiformes includes the single Family Luganoiidae which is represented by two genera from the marine Middle and Upper Trias (Brough 1939). The members are small, very advanced chondrosteans with fusiform bodies and somewhat dorso-ventrally compressed heads. The skull is characterized by a certain amount of fusion of the roofing bones. Thus in *Luganoia* Brough the parietals, dermopterotics and dermosphenotics have fused into a posterior bony plate and the frontals have also fused into an anterior plate which is distinctly narrow anteriorly. In *Besania* Brough all these elements have fused into a single bony sheet. The opercular and subopercular are of approximately the same size and form a semicircular opercular cover, with a straight anterior border. The suspensorium is inclined forwards as in the semionotids (holosteans), but the preopercular is still large and high as in the Colobodontidae and the Peltopleuriformes. The maxilla however is reduced in size and has lost its intimate connection with the other cheek bones, particularly the preopercular, and has migrated anteriorly to resemble closely that of the more advanced semionotids. The lepidotrichia of the unpaired fins are few in number and presumably, equalled their endoskeletal supports. The individual rays are stiff and unarticulated proximally. The hemiheterocercal tail is markedly rounded and its scale lobe very short. The lower jaw has the beginnings of a coronoid process. The scales are thick, enamelled and those of the anterior flank region elongated dorso-ventrally. These fishes stand on the threshold of the holostean grade of evolution but still retain sufficient chondrostean characters to be regarded as among the most advanced chondrosteans, just falling short of the holostean grade. The obvious chondrostean characters include the lack of an interopercular and the retention of a large plate-like preopercular with a series of triangular bones above its dorsal extremity. This order provides another example of parallel evolution.

Both *Luganoia* and *Besania* have pointed teeth along the jaw margins and although the gape is somewhat restricted they were probably quite voracious, surface to mid-water feeders. The Luganoiiformes have several features in common with the Peltopleuriformes, in particular the greatly elongated flank scales and the high, large preopercular, which is dorsally fragmented. This order shared a common origin with the Perleidiformes, Peltopleuriformes and Cephaloxeniformes.

Order PLATYSIAGIFORMES

Another order composed of a single family, the Platysiagidae, containing only one genus, *Platysiagum* Egerton. *Platysiagum* extends from the Middle Trias to the Lower Lias (Gardiner 1960, 1966*a*) and is essentially a marine form. It is of elongate fusiform shape with a deeply forked, equilobate tail (hemiheterocercal). The paired fins are holostean in structure, as in the previous order, and are of moderate size. All the fins have numerous small fulcra, and the lepidotrichia are stout, bifurcating and only distally articulated. The mandible has a broad coronoid process and the dentition consists of a series of large, conical, pointed teeth, interspersed with numerous, irregularly arranged smaller teeth, suggestive of a predaceous habit. The suspensorium is vertical, the maxilla palaeoniscoid in shape and the preopercular high, broad and dorsally fragmented, similar to that of the Colobodontidae. The Platysiagiformes have basically the same skull structure as the Colobodontidae but differ in possessing an incipient interopercular and in the absence of a suborbital series. This order was probably derived from the Colobodontidae (Perleidiformes) and represents another chondrostean order which has moved independently towards the holostean grade of structure.

Order REDFIELDIIFORMES

The Order Redfieldiiformes includes the single family Dictyopygidae, which for a long time has been associated with the Colobodontidae in the Order Perleidiformes.

The Redfieldiiformes, however, can be distinguished from the Perleidiformes by the excess of rays over radials in both the dorsal and anal fins and in having often only one modified branchiostegal ray.

The origins of this order are somewhat obscure although the contemporaneous Dicellopygidae appears to have been derived from the same palaeonisciform stock (Gonatodidae–Commentryidae).

The Family Dictyopygidae is a fresh-water group, well represented in the Lower and Middle Triassic fresh-water beds of South Africa, Australia and North America (Brough 1931). The most primitive members of the Dictyopygidae exhibit the more conservative palaeoniscoid condition apart from the tail which is now hemiheterocercal. In the main the redfieldiids differ from the perleidids in that the dermal rays of the fin are more numerous than the endoskeletal supports and are also completely articulated. The snout still has the prominent palaeoniscoid rostrum and the rostro-premaxillo-antorbital is still a single bone in the primitive members. The suspensorium is oblique. However, Brough (1931) has shown that within the redfieldiids structural changes were taking place, so that the more advanced forms had come to resemble the perleidids much more closely. The suspensorium straightens and the lepidotrichia of the pectoral fin are undivided proximally, the caudal fin becomes less and less heterocercal and the lepidotrichia of the paired fins come to almost equal the endoskeletal supports. Of the sixteen or more described genera, eight are recorded from Australia and another five from South Africa. *Redfieldius* Hay is well known from the Upper Trias of South Africa and North America. The early redfieldiids are thus very similar to the predaceous palaeoniscoids, both in body shape, fin structure and dentitition, and presumably had very similar habits.

Order PHOLIDOPLEURIFORMES

This order ranges from the Lower to Upper Trias. It contains one family, the Pholidopleuridae, three members of which are marine and the fourth fresh-water (*Macroaethes* Wade). The pholidopleurids are small to moderately long, slender fishes. The dorsal and anal fins are far back, the origin of the anal being anterior to that of the dorsal. The lepidotrichia of the unpaired fins are more numerous than the endoskeletal supports and all are articulated and distally bifurcated. The tail is hemiheterocercal, deeply cleft and with a reduced scaly lobe. The suspensorium is almost vertical to moderately oblique, the orbit large and the preopercular high and perleidid in make up. The frontals are very large and the rostrum is blunt. The parietals are considerably subdivided into a series of elements. The maxilla has the normal palaeoniscoid proportions, the teeth are small and pointed and the scales thin. *Australosomus* Piveteau from the Lower Triassic, marine deposits of Madagascar, Greenland and Spitsbergen was a wide-ranging species and it is also recorded from the Lower Trias of Tanzania, while *Macroaethes* Wade is confined to Middle Triassic, fresh-water deposits of Australia. This again is another chondrostean order whose affinities remain obscure, but which possibly originated from the same palaeoniscoid stock as the Redfieldiiformes.

Order PARASEMIONOTIFORMES

This order is probably the most important of the more advanced chondrostean orders since it provides the almost ideal stepping-stone to the more advanced holosteans and halecostomes. The order contains two families, the Parasemionotidae and the Tungusichthyidae, which are confined to the marine Lower Trias.

The Family Tungusichthyidae, containing the single genus *Tungusichthys* Berg (Berg 1941) from the Lower Trias of the Tunguska Coal Basin, Siberia, is not well known. The caudal fin still has a pronounced scaly lobe but superficially tends towards the homocercal condition, being only weakly cleft. The fins are distinctly holostean in make-up with few rays and these are bifurcated but only distally articulated. The suspensorium is vertical and the preopercular narrow as in the caturids; in this respect it differs from the Parasemionotidae. The maxilla is thin and reduced, very much holostean in appearance and with a supramaxillary in articulation; the interopercular is small.

The Family Parasemionotidae contains eight genera from the Lower Trias of Madagascar and Greenland. They represent a fairly uniform group but with considerable variation in the preopercular and snout regions (Lehman 1952).

Apart from the skull, the Parasemionotidae are completely holostean, although the scaly lobe of the hemiheterocercal tail still extends almost halfway along the dorsal lobe. The body shape, size, scaling and nature of the paired and unpaired fins are all distinctly holostean and halecostome. In the skull the roofing bones correspond in basic structure and arrangement to those of the early holosteans and halecostomes. In the cheek region the maxilla is freed from the preopercular while the opercular series includes a true interopercular. In both these features the Parasemionotidae closely approach the holosteans. Only in the size and shape of the preopercular and absence of a true suborbital series do the Parasemionotidae fall short of the holostean and halecostome grades. The preopercular is still large and broad medially and would need to become more curved antero-ventrally and broadened in that region to approach the condition found in the halecostomes. However, Lehman (1952) has shown that within the Parasemionotidae suborbitals are being formed by anamestic fragmentation of the anterior part of the preopercular. Therefore, he concludes that the Parasemionotidae are probably ancestral to the caturids. Further, Gardiner (1960) has shown the remarkable similarity that exists between the Parasemionotidae on the one hand and the halecostomes on the other.

The actual origin of the Parasemionotiformes is less clear. Of the known chondostrean families the Aeduellidae (Palaeonisciformes) look the most likely ancestors. The family includes the two genera *Aeduella* Westoll and *Westollia* White & Moy-Thomas from the Lower Permian of Autun and Thuringia respectively. These are characterized by the upright nature of the suspensorium, the reduction of the posterior expanded portion of the maxilla, and the shape and size of the preopercular. The body is of the right shape and proportions to have given rise to the Parasemionotiformes although the fins are distinctly palaeoniscoid. There is no interopercular. Thus it seems that the Aeduellidae and the Parasemionotiformes shared a common ancestry in the upper Carboniferous.

Order PTYCHOLEPIFORMES

Members of this order are first encountered in the Middle Trias and the order survived into the Upper Lias. The order is represented by a single family, the Ptycholepididae, containing the single genus *Ptycholepis* Agassiz.

Ptycholepis is a marine form and ranges in size from small to large (some 60 cm.). It is elegantly fusiform with an acutely pointed snout (Gardiner 1960). The caudal fin is deeply forked and hemiheterocercal. The pectoral and pelvic fins are well developed, the dorsal and anal fins are triangular, the former opposed to the pelvics, the latter smaller and remote. The lepidotrichia of the unpaired fins are few in number and completely articulated and distally bifurcated, nearly equalling their endoskeletal supports in number. The suspensorium is almost vertical, the gape wide and the orbit large. The dentition consists of two series of small, close-set teeth and these fishes were presumably mid-water, plankton feeders. The frontals are large and elongate, making up the major portion of the skull roof. The skull roofing bones are distinctly ornamented with high ridges of enamel. The snout is produced into a blunt rostrum with a prominent postrostral present. The opercular is large and quadrangular, the scales thick, longer than wide and much elongated in the ventral region.

Because of the holostean-like character of the body and fins, this genus has in the past been grouped in the Holostei, but the absence of an interopercular, the possession of a palaeoniscoid-type maxilla and preopercular (covered with suborbitals in later species) and other obvious chondrostean characters of the skull, such as the snout, show that *Ptycholepis* is a representative of yet another independent line from the palaeoniscoids, which has not yet quite reached the holostean level. Brough (1939) has shown that the Ptycholepiformes can be directly derived from the earlier Boreosomidae.

Order BOBASATRANIIFORMES

The bobastraniids form a compact little group found only in the marine Lower Trias. The single Family Bobasatraniidae has representatives from Spitsbergen, Madagascar, Greenland and North America.

The bobasatraniids resemble the later pycnodonts in many respects but are in no way related to them. The bobasatraniids are an offshoot from the same palaeoniscoid stock which gave rise to the amphicentrids, and they died out without giving rise to any other group. In general body-form the bobasatraniids resemble the earlier Amphicentridae, particularly in the make-up of the shoulder girdle and the unpaired fins and in the much deepened, laterally compressed body. The lepidotrichia of the fins are slightly more numerous than the endoskeletal supports and the dorsal and anal fins are long as in some species of *Platysomus* Agassiz. However the median fins are holostean in form while the opercular apparatus is peculiar. The opercular is small with a much expanded preopercular plate below it and with the branchiostegal rays completely reduced. The clavicle has been lost.

Bobasatrania White (1932) has a modified crushing dentition reminiscent of that seen in *Chirodus*. The suspensorium is upright, the gape small, the pectoral fins long and the pelvics wanting. The dorso-ventrally deepened body, strongly forked heterocercal tail, long dorsal and anal fins and crushing dentition suggest that this was a browsing form probably feeding close inshore amongst corals.

Order DORYPTERIFORMES

The Order Dorypteriformes includes the family Dorypteridae which is represented by the single genus *Dorypterus* Germar from the marine Upper Permian (Gill 1925 ; Liu & Tseng 1964). *Dorypterus* shows many points of similarity to the Bobasatraniiformes and, like this order, was probably derived from the earlier Amphicentridae. There are close relationships between the axial skeleton and fin skeleton of *Dorypterus* and *Bobasatrania* White ; the expanded sinuous axonosts are in contact with one another, while the development of the body axis of the caudal fin is more or less identical in both. The bones of the upper jaw are similarly developed in *Dorypterus* and *Bobasatrania* and the pectoral girdles show many likenesses. However, despite these few similarities there are many divergent features ; no known bobasatraniid shows the extreme modifications of the skull found in *Dorypterus* and likewise the body of *Dorypterus* is not completely covered with thick scales (as in bobasatraniids). The scaling is reduced to the anterior portion of the trunk in *Dorypterus*. It would appear that the dorypterids and bobasatraniids must have come from the same early amphicentrid-like stock but both lines soon died out.

IV. CLASSIFICATION OF THE CHONDROSTEI

Class *ACTINOPTERYGII*

Subclass *CHONDROSTEI*

Order Palaeonisciformes

- Family Cheirolepididae Pander 1860
  - *Cheirolepis* Agassiz 1835
- Family Stegotrachelidae Gardiner 1963
  - *Stegotrachelus* Woodward & White 1926, *Moythomasia* Gross 1950, *Orvikuina* Gross 1953, *Kentuckia* Rayner 1951
- Family Osorioichthyidae nov.
  - *Osorioichthys* Casier 1954 (*Stereolepis* Casier 1952, *Stereolepidella* Whitley 1954)
- Family Tegeolepididae Romer 1945
  - *Tegeolepis* Miller 1892 (*Actinophorus* Newberry 1888), ?*Apateolepis* Woodward 1890, ?*Megapteriscus* Wade 1935, ?*Elpisopholis* Woodward 1908
- Family Carbovelidae Romer 1945
  - *Carboveles* White 1927, *Phanerosteon* Traquair 1881
- Family Gonatodidae nov.
  - *Gonatodus* Traquair 1877, *Drydenius* Traquair 1890, *Pseudogonatodus* nov.
- Family Gyrolepidotidae nov.
  - *Gyrolepidotus* Rohon 1889, *Palaeobergia* Matveeva 1958

Family Cosmoptychiidae Gardiner 1963
Watsonichthys Aldinger 1937, *Cosmoptychius* Traquair 1877

Family Acrolepididae Aldinger 1937
Acrolepis Agassiz 1833, *Acropholis* Aldinger 1935, *Acrorhabdus* Stensiö 1921, *Hyllingea* Aldinger 1935, *Plegmolepis* Aldinger 1937, *Reticulolepis* Aldinger 1937, *Mesonichthys* Gardiner 1963

Family Elonichthyidae Aldinger 1937
Elonichthys Giebel 1848 (*Ganacrodus* Owen 1867, *Propalaeoniscus* Pomel 1853), *Namaichthys* Gürich 1923

Family Rhadinichthyidae Romer 1945
Rhadinichthys Traquair 1877, *Cycloptychius* Young 1866, *Rhadinoniscus* White 1937, *Aetheretmon* White 1927, *Strepheoschema* White 1927, *Mentzichthys* Jubb 1965, *Eurylepidoides* Case 1935, *Ganolepis* Woodward 1893

Family Canobiidae Aldinger 1937
Canobius Traquair 1881, *Mesopoma* Traquair 1890, *Whiteichthys* Moy-Thomas 1942, ?*Aldingeria* Moy-Thomas 1942

Family Pygopteridae Aldinger 1937
Nematoptychius Traquair 1875, *Pygopterus* Agassiz 1833

Family Rhabdolepididae Gardiner 1963
Rhabdolepis Troschel 1857

Family Styracopteridae Moy-Thomas 1939
Styracopterus Traquair 1890 (*Fouldenia* White 1927), *Benedenius* Traquair 1878 (*Benedenichthys* Traquair 1890)

Family Cryphiolepididae Moy-Thomas 1939
Cryphiolepis Traquair 1881

Family Amphicentridae Moy-Thomas 1939
Chirodus M'Coy 1848 (*Amphicentrum* Young 1866, *Cheirodus* M'Coy 1855, *Hemicladodus* Davis 1884), *Cheirodopsis* Traquair 1881, *Eurynothus* Agassiz 1834 (*Eurinotus* Agassiz 1836, *Euronotus* Agassiz 1835, *Eurunotus* Pander 1860, *Eurynotus* Agassiz 1834, *Notaemon* Gistl 1848, *Plectrolepis* Egerton 1850), *Eurynotoides* Berg 1940, *Paraeurynotus* Chabakov 1927, *Globulodus* Münster 1842 (*Eurysomus* Young 1866, *Lekanichthys* Brough 1934), *Proteurynotus* Moy-Thomas & Dyne 1938, ?*Tompoichthys* Obruchev 1964

Family Platysomidae Young 1866
Platysomus Agassiz 1833 (*Stromateus* Blainville 1818), *Mesolepis* Young 1866 (*Pododus* Agassiz 1844), *Paramesolepis* Moy-Thomas & Dyne 1938, *Wardichthys* Traquair 1875, *Caruichthys* Broom 1913

Family Holuridae Moy-Thomas 1939
Holurus Traquair 1881, *Holuropsis* Berg 1947, *Palaeoniscinotus* Rohon 1890, *Peleichthys* Broom 1913, *Disichthys* Broom 1913

Family Cornuboniscidae White 1939
Cornuboniscus White 1939

Family Phanerorhynchidae Stensiö 1932
Phanerorhynchus Gill 1923

Family Trissolepididae Frič 1893
Sphaerolepis Frič 1877 (*Trissolepis* Frič 1893), *Sceletophorus* Frič 1894 (*Phanerosteon* Frič 1894, *Gymnoniscus* Berg 1936)

Family Birgeriidae Aldinger 1937
Birgeria Stensiö 1919 (*Xenesthes* Jordan 1907), *Ohmdenia* Hauff 1953

Family Atherstoniidae nov.
Atherstonia Woodward 1889 (*Hypterus* Owen 1876, *Broometta* Chabakov 1928)

Family Urosthenidae Woodward 1931
Urosthenes Dana 1848

Family Scanilepididae Romer 1945
Scanilepis Aldinger 1935, *Evenkia* Berg 1941

Family Amblypteridae Romer 1945
Amblypterus Agassiz 1833 (*Aedua* Sauvage 1890, *Archaeonichthys* Whitley 1940, *Archaeoniscus* Sauvage 1890, *Leiolepis* Goldenburg 1873), *Paramblypterus* Sauvage 1888 (*Amblypterops* Sauvage 1889, *Cosmopoma* Sauvage 1889, *Dipteroma* Sauvage 1889, *Geomichthys* Sauvage 1889), *Amblypterina* Berg 1940, *Tholonotus* Dunkle & Schaeffer 1956

Family Commentryidae Gardiner 1963
Commentrya Sauvage 1888 (*Elaveria* Sauvage 1888)

Family Lawniidae nov.
Lawnia Wilson 1953

Family Dicellopygidae Romer 1945
Dicellopyge Brough 1931, ?*Aneurolepis* White & Moy-Thomas 1941 (*Urolepis* Bellotti 1857)

Family Aeduellidae Romer 1945
Aeduella Westoll 1937, *Westollia* White & Moy-Thomas 1940 (*Lepidopterus* Pholig 1892)

Family Boreolepididae Aldinger 1937
Boreolepis Aldinger 1937

Family Palaeoniscidae Vogt 1852
Palaeoniscum Blainville 1818 (*Eupalaeoniscus* Rzchak 1881, *Palaeoniscus* Agassiz 1833, *Palaeothrissum* Blainville 1818, *Palaeomuzon* Weigelt 1930), *Pteronisculus* White 1933 (*Glaucolepis* Stensiö 1921), *Agecephalichthys* Wade 1935, *Myriolepis* Egerton 1864, *Trachelacanthus* Fischer de Waldehim 1850, *Gyrolepis* Agassiz 1833, ?*Gyrolepidoides* Cabrera 1944, *Turseodus* Leidy 1857, *Belichthys* Wade 1935, ?*Progyrolepis* Frič 1894, ?*Challaia* Rusconi 1946, *Leptogenichthys* Wade 1935

Family Cosmolepididae nov.
Cosmolepis Egerton 1854 (*Oxygnathus* Egerton 1854, *Thrissonotus* Agassiz 1844)

Family Centrolepididae Gardiner 1960
Centrolepis Egerton 1858

Family Coccolepididae Berg 1940
Coccolepis Agassiz 1844, *Browneichthys* Woodward 1889, *Sunolepis* Liu 1957, *Pteroniscus* Chekker 1848
Family Coccocephalichthyidae Romer 1945
Coccocephalichthys Whitley 1940 (*Coccocephalus* Watson 1925, *Cocconiscus* White & Moy-Thomas 1940)
Family Brachydegmidae nov.
Brachydegma Dunkle 1939
Family Boreosomidae nov.
Boreosomus Stensiö 1921 (*Diaphorognathus* Brough 1933), *Mesembroniscus* Wade 1935
Order Tarrasiiformes
Family Tarrasiidae Traquair 1881
Tarrasius Traquair 1881, *Palaeophichthys* Eastman 1907.
Order Haplolepiformes
Family Teleopterinidae Berg 1936
Haplolepis Miller 1892 (*Eurylepis* Newberry 1857, *Mecolepis* Newberry 1856, *Mekolepis* Newberry 1857), *Pyritocephalus* Frič 1894 (*Teleopterina* Berg 1936)
Order Saurichthyiformes
Family Belonorhynchidae Woodward 1888
Saurichthys Agassiz 1834 (*Belonorhynchus* Bronn 1858, *Giffonus* Costa 1862, *Ichthyorhynchus* Bellotti 1857, *Stylorhynchus* Martin 1873), *Saurorhynchus* Reis 1892 (*Belonostomus* Agassiz 1844, *Belonorhynchus* Bronn 1858, *Acidorhynchus* Stensiö 1925, *Gymnosaurichthys* Berg 1940)
Order Chondrosteiformes
Family Chondrosteidae Traquair 1877
Chondrosteus Egerton 1858, *Gyrosteus* Morris 1854, *Stichopterus* Reis 1909, *Strongylosteus* Jaekel 1929
Family Errolichthyidae Lehman 1952
Errolichthys Lehman 1952, *Psilichthys* Hall 1900
Family Peipiaosteidae Liu & Zhou 1965
Peipiaosteus Liu & Zhou 1965
Order Acipenseriformes
Family Acipenseridae Bonaparte 1831
Acipenser Linnaeus 1758, *Huso* Brandt 1833, *Kessleria* Bogdanon 1882 (*Hemiscaphirhynchus* Berg 1911, *Pseudoscaphirhynchus* Nicolsky 1900), *Protoscaphirhynchus* Wilimovsky 1956, *Scaphirhynchus* Heckel 1835
Family Polydontidae Bonaparte 1838
Polyodon Schneider 1801, *Palaeopsephurus* MacAlpin 1947, *Pholidurus* Woodward 1889, *Psephurus* Guenther 1873, *Crossopholis* Cope 1883
Order Polypteriformes
Family Polypteridae
Polypterus Sainte-Hilaire 1802 (Lacépède 1803), *Erpetoichthys* Smith 1865 (*Calamoichthys* Smith 1866)

Order Perleidiformes

Family Colobodontidae Stensiö 1916

Colobodus Agassiz 1844, *Crenolepis* Carus 1888 (*Crenilepis* Dames 1888, *Crenilepoides* Strand 1929), *Meridensia* Stensiö 1916, *Perleidus* Alessandri 1910, ?*Thoracopterus* Bronn 1858, ?*Gigantopterus* Abel 1906, *Meidiichthys* Brough 1931, *Mendocinichthys* Whitley 1953 (*Mendocinia* Bordas 1944), *Tripelta* Wade 1940, *Chrotichthys* Wade 1940, *Zeuchthiscus* Wade 1940, *Pristisomus* Woodward 1890, *Manlietta* Wade 1935, *Procheirichthys* Wade 1935, *Dimorpholepis* Teixeira 1947, *Engycolobodus* Oertle 1927, *Dollopterus* Abel 1906, *Albertonia* Gardiner 1966

Family Aetheodontidae Brough 1939

Aetheodontus Brough 1939

Family Cleithrolepididae Wade 1935

Cleithrolepis Egerton 1864, *Cleithrolepidina* Berg 1955, *Hydropessum* Broom 1909, *Dipteronotus* Egerton 1854

Order Luganoiiformes

Family Luganoiidae Brough 1939

Luganoia Brough 1939, *Besania* Brough 1939

Order Peltopleuriformes

Family Peltopleuridae Brough 1939

Peltopleurus Kner 1866, *Placopleurus* Brough 1939

Family Habroichthyidae nov.

Habroichthys Brough 1939

Order Cephaloxeniformes

Family Cephaloxenidae Brough 1939

Cephaloxenus Brough 1939

Order Platysiagiformes

Family Platysiagidae Brough 1939

Platysiagum Egerton 1872

Order Redfieldiiformes

Family Dictyopygidae Hay 1889

Redfieldia Hay 1899 (*Catopterus* Redfield 1837), *Dictyopyge* Egerton 1847, *Daedalichthys* Brough 1931, *Sakamenichthys* Nauche 1959, *Helichthys* Broom 1909, *Atopocephala* Brough 1934, *Brookvalia* Wade 1935, *Beconia* Wade 1935, *Dictyopleurichthys* Wade 1935, *Geitonichthys* Wade 1935, *Molybdichthys* Wade 1935, *Phlyctaenichthys* Wade 1935, *Schizurichthys* Wade 1935, *Ischnolepis* Haughton 1934, *Sinkiangichthys* Liu 1958, *Pseudobeconia* Bordas 1944, ?*Rushlandia* Bock 1959

Order Pholidopleuriformes

Family Pholidopleuridae Wade 1932

Australosomus Piveteau 1930, *Pholidopleurus* Bronn 1858, *Macroaethes* Wade 1932, *Arctosomus* Berg 1941 (*Neavichthys* Whitley 1951)

Order Ptycholepiformes

Family Ptycholepididae Brough 1939

Ptycholepis Agassiz 1833

Order Dorypteriformes
Family Dorypteridae Gill 1925
Dorypterus Germar 1842

Order Bobasatraniiformes
Family Bobasatraniidae Stensiö 1932
Bobasatrania White 1932 (*Lambeichthys* Lehman 1956), *Ecrinesomus* Woodward 1910

Order Parasemionotiformes
Family Parasemionotidae Stensiö 1932
Parasemionotus Piveteau 1929, *Stensionotus* Lehman 1952, *Watsonulus* Brough 1939, *Jacobulus* Lehman 1952, *Thomasinotus* Lehman 1952, *Ospia* Stensiö 1932, *Broughia* Stensiö 1932, *Helmolepis* Stensiö 1932
Family Tungusichthyidae Berg 1941
Tungusichthys Berg 1941

Chondrostei incertae sedis

Anaglyphus Rzehak 1881, *Anatoia* Rusconi 1946, *Caminchaia* Rusconi 1946, *Cenchrodus* Meyer 1847, *Cenechoia* Rusconi 1946, *Cephaliscus* Whitley 1940 (*Cephalacanthus* Beyrich 1848), *Echentaia* Rusconi 1946, *Guaymayenia* Rusconi 1946, *Hemilopas* Meyer 1847, *Neochallaia* Rusconi 1949, *Nephrotus* Meyer 1851, *Omphalodus* Meyer 1847, *Oxypteriscus* Matveeva 1958, *Pasambaya* Rusconi 1946, *Schigospondylus* Frič & Bayer 1902.

V. SUMMARY

This paper is the second of a series intended to form the basis for a revision of the palaeoniscoid fauna of the British Carboniferous. The type species of three genera from this fauna are redescribed and for comparative purposes two other type species from the Upper Carboniferous of Czechoslovakia.

Eight new Palaeonisciform families are erected. They are the Osorioichthyidae which appears to be an independently derived side line from the ancestral stock; the Gonatodidae, a family close to the Acrolepididae and to the Amblypteridae; the Gyrolepidotidae allied to the Acrolepididae–Elonichthyidae complex; the Atherstoniidae, a family close to the Trissolepididae; the Lawniidae which was probably derived from the Gonatodidae; the Cosmolepididae, Brachydeymidae and the Boreosomidae. One other new chondrostean family is proposed, the Habroichthyidae which belongs to the Peltopleuriformes.

A new genus *Pseudogonatodus* is erected for *Gonatodus parvidens* Traquair (1892) and it is also used to include *Gonatodus macrolepis* Traquair (1877).

The classification and evolution of the Palaeonisciformes is discussed and since all the chondrostean orders stemmed from the Palaeonisciformes, the subsequent evolution of the Subclass Chondrostei is outlined and a complete classification of the Subclass is attempted.

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VII. LETTERING USED IN TEXT FIGURES

Ang	angular	mp	median pit line
Ant	antorbital	Mx	maxilla
ap	anterior pit line		
Art	articular	Na	nasal
		na_1	anterior nasal aperture (nostril)
Br	branchiostegal ray	na_2	posterior nasal aperture (nostril)
can.W	canals of Williamson	o	pore
Cl	cleithrum	Op	opercular
Clav	clavicle	orp	postmaxillary sensory line
Cor	coronoid		
c.sp	cell spaces	Pa	parietal
		Pop	preopercular
d	dentine	pp	posterior pit line
Den	dentary	Ptr	postrostral
Dpt	dermopterotic		
Dsp	dermosphenotic	r	ridges of enamel
d.t	dential tubules	r.can	radial canal
Dyh	dermohyal	r.cr.con	radial cross connection
		R.pmx	rostro-premaxillary
e	enamel	R.pmx.ant	rostro-premaxillo-antorbital
Exsc	extrascapular		
		Sbo	suborbital
fe	fenestra	Scl	supracleithrum
Fr	frontal	sc.r.	sclerotic ring
		Sh.f	Sharpey's fibres
Gu	gular plate	So	supraorbital
		soc	supraorbital sensory canal
hc	supramaxillary sensory line	Sop	subopercular
h.la	horizontal bone lamellae	Ssc	suprascapular
h.v.can	horizontal network of canals		
Hy	hyomandibular	B.M.N.H.	British Museum (Natural History), London
Inf	infraorbital	R.S.M.	Royal Scottish Museum, Edinburgh
infc	infraorbital sensory canal		

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